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**FOR THE COMMANDER**

William F. Wittman

for **KENNETH R. BOFF, Chief**
Human Engineering Division
Armstrong Laboratory

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We hereby approve the Dissertation

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# ABSTRACT


## THE SPATIOTEMPORAL CHARACTERISTICS OF VISUAL MOTION PRIMING

by Alan Roger Pinkus

A motion signal that is produced from a sine-wave luminance grating which has undergone an abrupt 90-degree phase shift (frames 1 to 2) can serve as a priming signal that disambiguates motion of a second, 180-degree (counterphase) shift (frames 2 to 3). Four experiments investigated the spatiotemporal characteristics of this phenomenon which is termed visual motion priming (VMP). Experiment 1 varied the phase-shift magnitude of the priming signal from 22.5 through 157.5 degrees. This resulted in an inverted U-shaped half-sine function that peaked at [illegible] degrees with 93.5% priming. Experiment 2 varied frame 2 duration (192, 384, 768, and 1530 ms), spatial frequency (0.7, 1.4, and 2.8 cycles/degree), and used 19 or 48% contrast for the 3 frames. VMP decreased monotonically from about 94% at 192 ms to near 50% (chance level) at 768 and 1530 ms. Duration and spatial frequency were significant, but contrast had no systematic effect. Experiment 3 varied the ratio of frame 1 contrast (4, 6, 13, 19, 30, 48%) relative to frames 2 and 3, where both of the latter two frames had either 19 or 48% contrast. Several effects were observed. When the ratio of the contrasts between frames 1 and 2 was largest (4-48-48% contrast for frames 1-2-3, respectively), VMP was lowest at 82%. A smaller initial ratio, but a lower overall contrast level (4-19-19% contrast), resulted in a higher VMP of 91.5%. As the priming contrast ratios decreased to 1:4 or less, irrespective of overall contrast level, VMP quickly asymptoted. The results indicated that the strength of the priming signal was largely determined by the contrast ratio and not absolute contrast or their product. Experiment 4 used a

split-field presentation as a control to discount eye movement effects, where VMP was either outward or inward. Observers spontaneously saw both types of VMP. The results from these studies are analyzed in terms of the extensions and limitations of the elaborated Reichardt detector model (van Santen & Sperling, 1984, 1985) and the summation of motion signals over time.

# THE SPATIOTEMPORAL CHARACTERISTICS OF VISUAL MOTION PRIMING

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I draw strength from their nurturance and love.

I dedicate this dissertation to my daughter

*Barrie Lane*

The Light of My Life

# INTRODUCTION

*Visual Motion Priming*

Real motion can be observed when an object is continuously displaced through space over time. Given the appropriate spatial and temporal qualities, successive presentations of discrete stationary stimuli (e.g. movies) also appear to be moving, and the sensation so produced is called apparent motion (Wertheimer, 1912, cited in Anstis, 1986). The visual motion priming (VMP) paradigm is based on the interaction of unambiguous and ambiguous apparent motion signals (Pantle, Pinkus, & Strout, 1992). Unambiguous apparent motion is illustrated in Figure 1 by a space-time plot of a sine-wave (SW) grating that undergoes an abrupt 90-degree phase shift to the right. The x-axis is the space dimension which represents a luminance scan across the SW pattern. The y-axis denotes the luminance changes over instances of time. In Figure 1, a uniform field that has the same space-average

Insert Figure 1 about here

luminance as the SW, is shown both before and after the gratings. The phase-shifted grating generates a motion signal that causes motion to be perceived in the rightward direction nearly 100% of the time. By comparison, the same grating can be shifted 180 degrees (counterphase shift), as shown in Figure 2, and in isolation, its direction of motion would appear to be rightward or leftward with nearly equal probabilities. The direction of motion is perceptually ambiguous. In the Fourier

Insert Figure 2 about here

domain, a counterphase grating is equivalent to the sum of two identical (one-half contrast) SW gratings that are moving in equal but opposite directions; hence neither left nor right motion signals predominate (Sekuler & Levinson, 1977). In VMP, an unambiguous 90-degree jump precedes a counterphase jump (see Figure

3). The first motion signal presumably causes a temporary directional bias that persists for a finite time period. If there is sufficient residual bias when the

Insert Figure 3 about here

second jump occurs, it is seen to move in the same direction as the first jump. VMP has taken place when both jumps are observed and the second jump moves in the same direction as was physically represented by the first jump.

A minimum of two frames are required for apparent motion. The instant frame 2 is presented, a motion signal arises as the result of the neural network becoming biased in one direction. The bias immediately begins to decay. If the priming signal is progressively weakened, for example, by increasing frame 2 duration, there is a corresponding lower amount of residual bias. The observer begins to see the second jump move in the opposite direction of the first jump more often. The percentage of the "same direction" responses to the second jump decreases and becomes equal to the "opposite direction" responses, which is equivalent to counterphase signals in isolation. In summary, the priming signal constitutes a "biaser" of the motion system and the counterphase shift is the "probe" of the residual imbalance. The extent to which the probe is disambiguated (a significant difference from 50% probability) reflects the amount of residual bias (or imbalance) due to the action of the priming signal.

In order to overcome the disadvantages of other priming studies, the present studies employed SW stimuli. The use of SW gratings in VMP allows simple, independent manipulation of spatial frequency, contrast, and phase relationships for the direct application to and evaluation of computational models.

## *Empirical Background*

### *Extrapolation of Motion Path*

Several studies, as well as VMP, have relied upon biasing an observer's perception of an ambiguous stimulus. Investigations of the extrapolation of motion paths, also referred to as visual momentum or inertia, depended on the ambiguous nature of bistable-dot figures. Ramachandran and Anstis (1983) presented observers with four dots arranged in a diamond shape (see Figure 4a). Alternation of the top/bottom pair (frame 1) with the left/right pair (frame 2) resulted in a

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Insert Figure 4 about here

---

bistable percept. Dot pairs moved in either a northwest-southeast or a northeast-southwest direction. Movement in the two directions was equally probable and mutually exclusive. Closer spacing along one diagonal orientation (D1 or D2) caused a bias allowing one of the percepts to predominate. The diamond was then embedded in two longer rows of dots (see Figure 4b). Even though the distances were manipulated to cause both "streaming" or "bouncing" percepts, observers saw only streaming. Sequences of dots exerted a strong effect on the perceived direction of motion of the embedded dot figure. When the priming dots were occluded (frames 1, 2, 5, 6) the diamond-shaped, bistable percept became equally probable again. Ramachandran and Anstis (1983) called this phenomenon extrapolation of motion path, and believed it to be one method the visual system uses to solve the correspondence problem (Ullman, 1979). The problem of motion correspondence occurs when the system must determine which are the correct matches among numerous possible mismatches. Similar phenomena were investigated by Eggleston (1984) and by Anstis and Ramachandran (1987). Eggleston (1984) examined the effects of two additional priming dots (frame 0) on an embedded square-shaped, bistable-dot figure (same as Figure 4c, but rotated 45 degrees). When he varied the interstimulus interval between the priming and test dots, he found strong priming up to 500 ms, but the effect disappeared at 1000 ms. In a similar study, Anstis and Ramachandran (1987) also varied the interstimulus interval between the priming dots and first test dots of bistable-diamond figures (see Figure 4c). Percent visual inertia was highest at 33 ms but quickly asymptoted between 500 and 1000 ms. Their result was essentially the same as that found by Eggleston (1984). In addition, they varied the angle between the priming and test dots. The strength of the visual inertia effect diminished as the off-axis priming angle increased. They argued that the visual system used the priming dots to extrapolate motion path to achieve computational economy.

All of these phenomena are analogous to the VMP effect in that apparent motion sequences are used to bias the subsequent perception of ambiguous figures. However, dot stimuli are too complex to allow systematic investigation of critical spatiotemporal parameters. Dots have a broad spatial frequency spectrum. When dot size or spacing are changed, many different spatial frequencies and phase relationships covary, complicating interpretation within motion-from-Fourier-components models.

*Sequential Recruitment*

Motion path experiments and VMP can be placed within the general context of the combination of motion signals over time. Nakayama and Silverman (1984) investigated the effect of increasing the number of random-dot cinematogram (RDC) frames on the upper displacement threshold for coherent motion, or $D_{MAX}$. Incoherent motion is the result of the visual system's inability to resolve the formidable correspondence problem imposed by alternating fields of RDCs. $D_{MAX}$ for RDCs is about 15 arc minutes (Braddick, 1974). When they introduced a pause halfway between the total distance and thereby caused two jumps, $D_{MAX}$ doubled.

This doubling occurred over the rather large range of pause durations of 10 to 400 ms. Between 10 and 100 ms, the upper displacement limit was extended considerably but then fell back down to two times $D_{MAX}$. They interpreted the overshoot as physiological summation or sequential recruitment, and not probability summation. McKee and Welch (1985, p. 245) provided a succinct definition of "simple physiological summation, [where] signals are summed within neurally defined spatial and temporal limits such that the detectability of each component is highly correlated with the detectability of other components and depends on the inherent noise of the whole pool." When successive looks at motion are integrated within a given time frame, more information is available for the resolution of ambiguity and the establishment of correspondence.

In a study similar to Nakayama and Silverman (1984), Snowden and Braddick (1989) measured the effect of the number of RDC frame displacements on $D_{MAX}$. They found that the upper displacement limit asymptoted at about 150% of a single-step $D_{MAX}$ with 4 to 6 displacements. They viewed their results as the possible interaction and mutual facilitation of many motion detectors. Facilitation would occur ahead of the projected path of the moving object. This is similar to the dot priming found in the extrapolation of motion path study by Ramachandran and Anstis (1983).

Additional evidence that the combination of motion signals over time is physiological in nature, and not probability summation alone, was provided by McKee and Welch (1985). They measured velocity-discrimination thresholds for a vertical line presented in both apparent motion (9'steps/10 ms) and continuous motion (15 degrees/sec), as a function of the total sequence duration. As duration increased, the observer saw either more apparent motion frames or a longer view of the continuously moving line. They found that velocity-discrimination thresholds improved as duration increased for both types of motion. For the apparent motion sequences, the largest improvement was between frames 2 and 3. Performance quickly asymptoted by 5 to 8 frame presentations. They constructed special line sequences to determine whether probability summation could account for their results. Temporal sequences of lines that combined orthogonal directions of motion did not reduce thresholds. McKee and Welch (1985) concluded that sequential recruitment was due to physiological summation that occurred along the motion path.

VMP is distinctive in that it is not confounded by possible probability summation effects. Although, priming is analogous to sequential recruitment where signals are combined over time, it does not compare the effectiveness of multiple signals versus one, but looks at changes in the perception of one signal. Moreover, VMP relies on the fact that the second signal is ambiguous, which provides absolutely no net directional signal or position cues. The extent to which the counterphase signal is disambiguated can form a metric for the strength of and the persistence of the biasing signal. A detailed analysis of a possible basis for priming signals will be presented in the General Discussion section after the empirical results of experiments on VMP are described.

## *Theoretical Background*

### *Directionally-Selective Motion Mechanisms*

It is known that presenting the visual system with stimuli that are moving in one direction causes directionally-tuned mechanisms to be selectively adapted. Viewing a continuously moving SW grating creates an imbalance between mutually-opposing mechanisms. When motion stops, the opposite direction temporarily predominates, with a resulting motion aftereffect or MAE (Sekuler, Pantle, & Levinson, 1978). Aristotle was the first to report this effect after prolonged viewing of a stream, but he was wrong as to the direction (Anstis, 1986). Addams (1834, cited in Sekuler, Pantle, & Levinson, 1978) correctly observed the direction of the MAE after extended gazing at a waterfall. MAEs have been extensively investigated (Levinson & Sekuler, 1975; Pantle, 1974; Pantle & Sekuler, 1969; Sekuler & Pantle, 1967) and provide another line of converging evidence for the biasing of directionally-selective motion mechanisms. In this respect, MAE and VMP are similar. The MAE, though, is the result of an imbalance caused by neural fatigue. By comparison, VMP is the result of a short-term directional imbalance produced by the persistence of a priming signal.

### *Motion Models*

Barlow and Levick (1965) measured the frequency of retinal ganglion cell action potentials while moving spots of light across a rabbit's visual field. Single-cell recordings revealed cell responses that increased and decreased with respect to baseline levels when stimuli were moved in preferred and null (opposite) directions, respectively. In addition, impulse rates of cells stimulated in the preferred direction, temporarily fell after cessation of motion. An imbalance is caused by sub-baseline responses of directionally-tuned cells following prolonged stimulation. This is evidence for a physiological basis of MAEs where there is a temporary imbalance between mutually-opposing, directionally-tuned, motion-sensitive mechanisms.

Barlow and Levick (1965) hypothesized several possible mechanisms of directional selectivity, the simplest involving a luminance gradient (e.g. a black/white step function) moving past two spatially separated retinal receptor units. When stimulated in the preferred direction, excitatory signals from the first unit would arrive before that of a delayed inhibitory signal from the second unit. In the null direction, the inhibitory signals precede and effectively cancel the latter excitatory influences. They also found that smaller subregions duplicated the directionality of the larger receptive field. The cells responded more strongly to a sequence of small lights than to a single larger spot of light, when moved within the same field size.

Numerous other motion detector models have been developed, several of them modifications and extensions of the autocorrelation technique used by Reichardt (1961, cited in van Santen & Sperling, 1984) to describe insect vision. Its basic form is shown in Figure 5. First, a moving luminance gradient passes by two

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Insert Figure 5 about here

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spatially separated retinal receptors. In the preferred direction, the signal from the first receptor is delayed before being combined through multiplication with the second receptor's signal. When correlated signals are multiplied, there is an increase in the output signal, whereas uncorrelated signals (or none at all) result in a decrease in the output. Infinite time-averaging integration filters provide a smoothing function. Outputs from two such directional subunits, each having opposite preferred directions (in Figure 5, solid lines are rightward and dotted lines leftward), are then subtracted to obtain the detector's opponent-energy output. The activity in one subunit is evaluated relative to its opposite subunit. A positive output would indicate one direction of motion; a negative value, the opposite direction.

The Reichardt detector is adequate to explain certain aspects of insect vision but requires modification to correct for known spatiotemporal characteristics of human vision. For example, if a periodic pattern such as a luminance-defined SW grating is moved at a constant speed across the detector, the output would indicate its direction. However, if a grating of a sufficiently high spatial frequency, moving at the same speed and direction, were passed over the detector, it could indicate the opposite direction. The same type of error could occur if a grating of a given spatial frequency were moved at ever increasing speeds. Even though the grating traveled in only one direction, the detector would indicate cyclic reversals of motion. This is termed aliasing, but it is not a property of the human visual system (van Santen & Sperling, 1984). The Reichardt detector is susceptible to both spatial and temporal aliasing. The model can be corrected by placing spatial and temporal filters after the receptors (see Figure 6). Spatial aliasing can be corrected by using

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Insert Figure 6 about here

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two filters with impulse responses that are Gabor functions. Temporal aliasing is corrected by delaying the first receptor's signal by a relatively long-duration (slow) temporal filter. This signal is then combined through multiplication with the second receptor's signal, that passed through a short-duration (fast) filter. Both of these filters have biphasic temporal impulse responses which first have an excitatory phase followed by an inhibitory phase, but with different durations. The model retains the temporal integration filters after the multiplication but before the subtraction stages. These filters provide infinite-time averaging which eliminates time-dependent components. The revised model is termed an elaborated Reichardt detector or ERD (van Santen & Sperling, 1984, 1985). Adelson and Bergen (1985) and Watson and Ahumada (1985) have developed motion energy models which differ in computational details, but van Santen and Sperling (1985) demonstrated that given the appropriate filter modifications, the energy and correlation models are formally equivalent.

Here it is assumed that VMP is the consequence of selective biasing of directionally-tuned motion subunits. The first motion signal causes one directional subunit to respond more vigorously than its complement. The time course of the response of the subunits is determined by the impulse response of the spatiotemporal filters. The temporal integration filters act to extend the persistence of the shorter responses in order to allow the integration of multiple temporal events. When the second ambiguous motion signal occurs within this integration period, they are summed. The perceived direction of the counterphase signal is disambiguated when there is sufficient integrated opponent energy remaining above some threshold. As discussed earlier, the model utilizes infinite time-averaging integration filters. If this type of filter is incorporated in practice, the summation of multiple motion signals as well as VMP, would take place over an infinite time period. A temporal filter having a finite-integration period is needed. If the time between the two motion signals exceeds the integration period, the first jump fails to affect the perception of the second. They are processed as two independent directional events.

VMP measures the impact the biasing signal has on motion mechanisms. Changing the characteristics of the priming signal allows one to evaluate the different stages within the motion model. For example, varying the priming signal's phase-shift magnitude provides a critical test of motion models that utilize spatiotemporal filters in quadrature phase. In another example, by increasing the time frame over which a biasing signal must exert its influence, VMP becomes a sensitive measure of the time course for a decaying directional signal.

This series of studies investigated the key spatiotemporal characteristics of the priming phenomenon. The goals of these four experiments were to: (1) measure the optimal priming phase-shift magnitude, (2) measure the persistence of the priming effect under different spatial frequency and contrast conditions, (3) characterize the priming strength under different contrast conditions, and (4) verify that VMP is not due to eye movements. For each individual experiment, the qualitative predictions of the standard ERD model are discussed and then compared to the empirical data. The precise character of the priming phenomenon, as well as suggested extensions and modifications for certain stages of the model, are held until the General Discussion section.

# GENERAL METHOD

The basic VMP paradigm involves the sequential presentation of three discrete frames (SW gratings) that result in apparent motion. The spatial frequency, contrast (Michelson), duration, and phase-shift magnitude of the gratings can be independently manipulated. Phase shifts among the gratings are instantaneous (zero inter-grating interval) and the time between trials is filled with a uniform field that has the same space-average luminance as the SW gratings. The SW grating in frame 1 is at zero degrees phase (arbitrary designation) followed by frame 2 which is the same grating phase shifted plus or minus a certain number of degrees. The physical direction of this phase shift is usually such that either an unambiguous leftward or rightward apparent motion signal is generated at the instant of the frame 1 to frame 2 transition. This priming signal creates a bias. The bias serves to disambiguate the perceived direction of a counterphase-grating jump that occurs at the frame 2 to frame 3 transition. Thus, if an observer's motion mechanisms are successfully biased, he/she sees the second jump move in the same direction. VMP requires the observer to see two distinct jumps with the second counterphase jump moving in the same direction as was physically presented by the first jump. Positive phase-shifted gratings move leftward and negative phase-shifted gratings move rightward.

*Observers*

The first three experiments used ten college age students each (50% males and 50% females, 30 total); 5 students participated in Experiment 4. All observers had normal or were corrected to 20/25 or better Snellen visual acuity.

*Apparatus*

Stimuli were displayed on a cathode-ray tube (CRT) monitor (Tektronix 604) that had a flat, 13.65 cm by 10.2 cm display face coated with a green P-31 phosphor (30 $\mu$sec persistence to 10%). The three-frame, apparent motion sequences were generated with a Motorola 6809 microprocessor-based computer, which had its input/output port connected to a high speed programmable peripheral interface (PPI) adapter circuit (Athey, 1984; Barden, 1982). An executive BASIC program controlled the generation, storage, and selection of up to 20, 3-frame sequences. The investigator selected a sequence, then BASIC used machine language (ML) subroutines to implement high-speed data readouts. The ML program (Leventhal, 1981) sent a synchronization (sync) pulse followed by 256 data points contained in memory, through the PPI to the sync circuits and an 8-bit, digital-to-analog converter (DAC). The sync pulse triggered the start of the horizontal ramp generator that swept the electron beam across the x-axis of the CRT. The beam was swept vertically (y-axis) with a free-running, 1.1 mHz triangular-waveform generator. A sequence of voltages from the DAC modulated the linear portion of the CRT z-axis, thereby controlling luminance (256 possible grayshades). Following the computer generated sync pulse, luminance data were written across the CRT in 6 msec (167 Hz). This resulted in the display of a one-dimensional pattern as controlled by the 256 algorithmically generated tabled values. If the values varied sinusoidally, a SW grating was displayed. The luminance values for frame 1 were repeatedly readout from memory to refresh the display until the desired frame duration was achieved; then the program moved to the next table of values for frame 2 and the readout started again. After the SW grating of frame 3 was displayed, the program began to read out another table that was filled with only one value, in order to generate the uniform field viewed between trials. This value was equal to the space-average value (luminance) of the

SW gratings. During the course of successive readouts, a ML subroutine compared the computer generated sync pulse to an externally generated, free-running sync pulse. When they were coincident, the DAC remained latched at the uniform field value and control of sync was switched to external hardware. The free-running sync was a few hertz faster to insure a quick and reliable transition. This process provided noise-free switching from the frame 3 SW grating to the uniform field and allowed the computer to return from ML subroutines to the executive BASIC program. Before the start of a new 3-frame sequence, this sync process was essentially reversed.

*Procedure*

The observer was seated in a dimly lit room, at a viewing distance of 137 cm from the monitor. The CRT was masked with a surround which contained a 10 cm circular aperture subtending 4.24 degrees. An observer viewed the display through this aperture which minimized position cues at the edges of the vertically oriented SW gratings. The display face was surrounded by a white, 244 cm high by 122 cm wide foam-core partition that was illuminated at 0.69 cd/m$^2$. The CRT monitor, computer and associated equipment, as well as the experimenter, were isolated from the observer by this partition. Both the uniform field intertrial intervals and the space-average luminance of the SW gratings were 4 cd/m$^2$. Instructions from a checklist were read to each observer (see Appendix 1). The key points were that he/she maintain a steady gaze on the CRT, visually stabilize (lock) onto the first grating, and passively allow the patterns to jump, without trying to track their direction. When the SW patterns disappeared, the observer verbally responded *right/right, right/left, left/right,* or *left/left.* The investigator recorded his/her response and selected the next randomly ordered pattern for presentation. Since

Experiment 4 used unique 1- and 2-jump split-screen presentations, the observer responded *out, in, out/out, out/in, in/out,* or *in/in.*

*Screening/Practice*

Each observer was given a screening/practice session. It consisted of both 1- and 2-jump stimuli that used 1.4-cycle/degree vertically oriented SW gratings. The 1-jump sequence was frame 1 at a 0-degree phase followed by frame 2 at either a rightward, +270-degree or a leftward, +90-degree phase. Both frames were of 1530 ms duration and 48% contrast. An observer reported either a single rightward or leftward jump. The 2-jump, VMP sequences were continual gratings at phases 0-270-90 degrees (a 90-degree right phase shift followed by a counterphase shift) or gratings at phases 0-90-270 degrees (a 90-degree left phase shift followed by a counterphase shift) having 1530-252-1530 ms durations, for frames 1-2-3, respectively. The observer verbally reported one of the four possible combinations of jump sequences. High (48-48-48% for frames 1, 2, and 3, respectively) and low (19-19-19%) contrast sequences were used to show the observer an example of how the patterns might vary. He/she was not told that there was a screening test, just a practice session. In order to pass the screening, he/she had to report without prompting, over 95% correct directions for the 1-jump trials and over 90% priming for the 2-jump trials. Priming was considered to have occurred when an observer saw the second jump move in the same direction as that physically presented by the first jump. Even though only the second jump was used to tally VMP scores, the observer had to see two jumps. Since priming is the interaction of two motion signals, both must be seen in order to measure the effect. The observer had to spontaneously see VMP and there was never any feedback given for his/her responses. Approximately 90% of all screened observers perceived the VMP phenomenon. Before any of the first three experiments began, the observer was shown a few examples of the test stimuli unique to a given block of trials.

The screening/practice for the split-screen presentation in Experiment 4 consisted of only 3, 1-jump sequences. The left and right halves of the SW grating moved simultaneously either 90 degrees outward, 90 degrees inward, or 180 degrees counterphase relative to the display center. The observer verbally responded with out or in. To pass the screening, he/she had to see over 95% of the motion jumps in the same direction as was physically presented by the 90-degree phase shifts and at about equally probable directions for the counterphase jump. These conditions reflect the observer's ability to discern the components of priming, not priming per se. He/she was never given feedback or allowed to practice split-field priming before the test.

All experiments were within-subject designs. For each of Experiments 1, 2, and 3, ten observers were shown 2 priming directions with 10 repetitions each, yielding 200 data points per experimental condition. Five observers were used in Experiment 4, so there were 100 data points per condition. All experimental conditions, directions, and repetitions were presented in a randomized order.

## EXPERIMENT 1: THE EFFECT OF FRAME 1 TO FRAME 2 PHASE-SHIFT MAGNITUDE ON VISUAL MOTION PRIMING

van Santen and Sperling (1985) analytically derived the ERD response for 2-jump, phase-shifted SW grating stimuli. The ERD output is dependent upon the product of the contrasts of the two gratings and the sine of the phase shift. Experiment 1 evaluated this relationship by fixing the contrasts and varying the phase-shift magnitude. The prediction was that VMP would follow a half cycle of the sine-wave function, with a peak corresponding to a 90-degree phase shift. Watson (1990) also derived predictions from quadrature models of motion (Adelson & Bergen, 1985; van Santen & Sperling, 1984, 1985; Watson & Ahumada, 1985) for two- and multiple-frame apparent motion displays. He found that for 2-frame presentations, the models predicted maximum response for 1/4-cycle displacements. Maximum response for multiple-frame displays depended upon frame rate. The 2-frame predictions of van Santen and Sperling (1985) and Watson (1990) are in agreement with the results found by Nakayama and Silverman (1985) and Baker, Baydala, and Zeitouni, (1989). Nakayama and Silverman (1985) varied the size of SW grating phase shifts and measured observers' contrast sensitivity for detecting motion direction. They found that for a range of spatial frequencies, the highest sensitivity occurred for a 90-degree shift. In a related study, Baker, Baydala, and Zeitouni (1989) varied the phase-shift magnitude of adapting SW gratings in apparent motion and measured the resultant MAE durations. The longest MAEs coincided with phase shifts just under 90 degrees. They concluded that their data supported the van Santen and Sperling (1984, 1985) motion model.

*Method*

Experiment 1 used 1.4-cycle/degree vertically oriented SW gratings presented at a 137 cm viewing distance. For frames 1-2-3, the contrasts were 19-48-48% and their durations were 1530-252-1530 ms, respectively. Before and after presentation of a 3-frame sequence, a uniform field was displayed. Both the SW gratings and the uniform field had the same space-average luminance (4 cd/$m^2$). The independent variable was the magnitude of the phase shift of the priming signal. The frame 1 to frame 2 phase shift was varied from -157.5 degrees through +157.5 degrees (0 degrees omitted) by 22.5 degree increments (1/16 of a cycle) yielding 14 conditions. The frame 2 to frame 3 phase shift was always 180 degrees. Positive and negative phase shifts represent the leftward and rightward physical directions of the priming signals, respectively. Presented in a randomized order, 7 phase shifts in 2 directions, 10 times each, yielded 140 stimuli for each of the 10 observers.

*Results and Discussion*

VMP occurred when the observer saw two jumps and the second jump moved in the same direction as that physically presented by the first jump. These responses were tallied for each of the 14 phase-shift conditions and divided by 10 to obtain the mean percent VMP for each observer. An AxBxS within-subjects analysis of variance revealed the following results. The effect of leftward versus rightward priming direction was not significant [$F(1,9) = 0.59$, $p = 0.46$]; the effect of phase-shift magnitude was significant [$F(6,54) = 6.80$, $p = 0.0001$]; and the direction by phase interaction effect was not significant [$F(6,54) = 1.97$, $p = 0.09$]. Figure 7 shows the mean percent VMP for all 10 observers plotted as a function of frame 1 to frame 2 phase-shift magnitude. The positive and negative

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Insert Figure 7 about here

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phase shifts were the leftward and rightward priming directions, respectively. Variations of phase-shift magnitude resulted in two, inverted U-shaped curves. Both had maxima of 94% mean priming at the leftward 90-degree and at the rightward -112.5-degree phase shifts. Since most observers exhibited some directional bias, it is not surprising that the curves did not peak at exactly the same point or have exactly the same shape. Given that no significant difference was found for priming direction nor a significant interaction between priming direction and phase-shift magnitude, and in order to obtain a better estimate of the phase effect, left and right scores were combined by averaging, to yield the composite VMP curve, shown in Figure 8. This method of calculating composite scores is

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Insert Figure 8 about here

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used for the successive analyses in Experiments 2 and 3. The inverted U-shaped composite curve has a maximum of 93.5% mean priming at 90-degree phase shift. Mean priming was 81.5% at 22.5 degrees and 82% at 157.5 degrees.

van Santen and Sperling (1985, p. 317) discussed the ERD predictions for a 2-frame presentation of phase-shifted SW gratings. Equation 1 is the result of their analytic derivation. An ERD's output is a positive function of the product of the

$$O_{l\text{-}r} = C_1 C_2 \text{sine}(\phi). \qquad \text{Equation 1}$$

Where: $O_{l\text{-}r}$ = Output of ERD (left subunit-right subunit)
$C_1$ = Contrast of the first frame SW grating
$C_2$ = Contrast of the second frame SW grating
$\phi$ = spatial phase shift

two contrasts and the sine of the spatial phase shift. This experiment held the contrasts constant at 19% and 48% (their product is 0.091) and varied the phase-shift magnitude. Equation 1 predicts the output as being a sine wave. To evaluate this prediction, the data shown in Figure 8 were plotted as a function of the sine of the frame 1 to frame 2 phase shifts, and a regression line was fit to the data by the Method of Least Squares. The slope coefficient was 17.66 and the intercept was 75.11. Figure 9 depicts the predicted ERD response from Equation 2 along with the empirical data as a function of the frame 1 to frame 2 phase shift.

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Insert Figure 9 about here

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The correlation between the predicted and the transformed data is 0.978 [ $p = 0.0001$], which demonstrates that the empirical VMP conform closely to the predictions of the standard ERD model.

$$y' = 17.66(\text{sine } x) + 75.11. \qquad \text{Equation 2}$$

Where: $y'$ = predicted ERD response
$x$ = frame 1 to frame 2 phase shift (degrees)

## EXPERIMENT 2: THE EFFECTS OF FRAME 2 DURATION, SPATIAL FREQUENCY, AND CONTRAST ON VISUAL MOTION PRIMING

The priming signal occurs at the instant of the frame 1 to frame 2 transition. This motion signal causes a directional bias which persists, but immediately begins to decay. The degree to which the counterphase signal is disambiguated indicates the amount of residual bias. As the frame 2 duration is increased, an increasingly smaller biasing signal remains to be integrated with the counterphase signal. When the integrated output falls below some threshold, the priming signal fails to disambiguate the second counterphase jump. As previously discussed, the ERD utilizes infinite-time averaging integration filters as a convenience to smooth time-varying components. Using this type of filter, the model predicts that the priming phenomenon would occur over an infinitely large frame 2 duration. Even though the directional subunit signals would have fully decayed (signals generated prior to the temporal integration stages in the model), the opponent energy to which they give rise would be integrated with the counterphase signal, no matter when the latter was presented. The combination of motion signals over an infinite-time period is not reasonable in a real-world context. This experiment varied the frame 2 duration in order to determine the time interval over which the priming signal's persistence can disambiguate a counterphase-shifted SW grating.

Spatial frequency was also independently manipulated in this experiment in order to evaluate its role in VMP. For static square-wave gratings, Lovegrove and Meyer (1984) measured the duration of visual persistence as a function of spatial frequency. They found that for 300 ms presentations of square-wave gratings, persistence decreased from 2 to 4 cycles/degree but then increased from 4 to 10 cycles/degree. Other studies (Bowling, 1981, cited in Lovegrove & Meyer, 1984) have compared square-wave and SW gratings and found no difference in their persistence. Lovegrove and Meyer (1984) attributed their results to neural summation. Note that the mechanisms responsible for visual persistence of statically presented gratings, may be fundamentally different from the persistence of direction-of-motion signals responsible for VMP.

The third independent variable was contrast. It was shown earlier from Equation 1 that the output of an ERD is the product of frame 1 and frame 2 contrasts, and the sine of the phase shift. Experiment 1 held the contrast product constant while varying the phase-shift magnitude. Conversely, this experiment fixed the priming phase shifts at the optimal values of plus and minus 90 degrees while varying the products. When frames 1-2-3 were 19-19-19% contrast, the contrast product for the priming phase shift was 0.036 and when the sequences were 48-48-48% contrast, the product was 0.230. The ERD output is lower for the 19% contrast condition. A lower detector output should result in a smaller residual biasing signal that will decay to threshold faster, resulting in less VMP.

*Method*

The independent variables for Experiment 2 were duration, spatial frequency, and contrast. Frame 2 durations were 192, 384, 768, and 1530 ms. Frames 1 and 3 were fixed at 1530 ms. The three spatial frequencies were 0.7, 1.4, and 2.8 cycles/degree. The 1.4-cycle/degree and 2.8-cycle/degree conditions were viewed at 137 cm and spatial frequency was changed electronically. The 0.7-cycle/degree condition was achieved by viewing the 1.4-cycle/degree grating at half the distance. For frames 1-2-3, the contrasts were either 19-19-19% or 48-48-48%, respectively. Phases of the frames were fixed at either 0-270-90 degrees (rightward priming) or 0-90-270 degrees (leftward priming). Since it was difficult to quickly change from one spatial frequency to another, 10 repetitions each of duration, contrast, and priming direction were randomized within a single block. The three spatial frequency blocks were then presented in a counterbalanced order across observers in separate sessions. To minimize fatigue, each observer was tested over two consecutive days. On the first day, the observer was given the screening/practice trials and one spatial frequency block. On the second day, he/she was tested using the remaining two spatial frequency blocks. Presented in a randomized order, 4 frame durations, at 2 contrasts, in 2 directions, and 10 repetitions for each of 3 spatial frequency blocks, yielded 480 stimuli for each of the 10 observers.

*Results and Discussion*

The results of Experiment 2 specify the mean percent priming as a function of frame 2 duration. Figure 10 also shows the priming for three different spatial frequencies at the low and high contrasts. All of the curves start near 94% priming

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Insert Figure 10 about here

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at 192 ms and then decrease monotonically to near 50% chance levels at 768 and 1530 ms. An AxBxCxS within-subjects analysis of variance revealed the following results. Increasing frame 2 duration significantly lowered VMP [$F(3,27) = 105.09$, $p = 0.0001$]; increasing spatial frequency caused a significant decrease in VMP [$F(2,18) = 4.51$, $p = 0.03$]; but VMP was not significantly affected by the two contrast levels used in the experiment [$F(1,9) = 2.66$, $p = 0.14$]. All interactions were not significant: duration by spatial frequency [$F(6,54) = 0.60$, $p = 0.73$], duration by contrast [$F(3,27) = 0.37$, $p = 0.78$], spatial frequency by contrast [$F(2,18) = 0.17$, $p = 0.85$], and duration by spatial frequency by contrast [$F(6,54) = 0.87$, $p = 0.52$]. Since contrast was not significant, the data were collapsed across this condition and replotted as shown in Figure 11. Collapsing across contrast clearly reveals the significant duration and spatial frequency effects.

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Insert Figure 11 about here

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The original ERD model places infinite time-averaging filters after the multiplicative, but before the subtractive stages, to eliminate time-dependent components of the directional-subunit signals. This kind of integrating function requires the ERD to predict that multiple signals would be combined over an indefinite time period. VMP would be independent of the time between the priming and counterphase jumps in the VMP paradigm. The second experiment revealed a finite time period over which the integration of motion signals takes place. VMP occurred within a window where its effect was strong near 190 ms and decreased monotonically to chance levels at about 770 ms. Each level of frame 2 duration was significantly different from all other levels [for all *t*-tests, $p \leq 0.004$]. Anstis and Ramachandran (1987) found similar results when they varied the interstimulus interval (from 33 to 1000 ms), between their priming and test dot frames (see Figure 4c). They found that percent visual inertia decreased monotonically and asymptoted between 500 to 1000 ms. In order to account for the decrease of VMP as a function of increased frame 2 duration, the infinite-time averaging filter needs to be replaced by a temporal integrator with a limited time constant. A temporal bandpass filter that has a Gaussian impulse response would serve the purpose. A detailed description of such a filter is left for the General Discussion.

Another finding of Experiment 2 was that an increase of spatial frequency significantly lowered VMP. The 0.7- and 2.8-cycle/degree conditions were significantly different from each other [$t(9) = -2.84$, $p = 0.02$], but they were not significantly different from the middle, 1.4-cycle/degree condition. This is similar to what Lovegrove and Meyer (1984) found in their visual persistence study where at spatial frequencies between 2 and 4 cycles/degree, persistence decreased before turning back upward. This decrease may not be theoretically important in a first approximation model of results, but the trend is noteworthy.

The ERD model predicts from Equation 1, that the higher the contrast product, the higher the output. Presumably, there would also be a correspondingly higher percentage of VMP. This result was not found. The two contrasts used in this experiment had no significant main or interactive effect on VMP. Due to this failure of the standard ERD model, Experiment 3 was conducted to more systematically investigate the effects of contrast.

## EXPERIMENT 3: THE EFFECTS OF BIASER AND PROBE CONTRASTS ON VISUAL MOTION PRIMING

Experiment 1 was undertaken to evaluate the effects of phase-shift magnitude while holding contrast constant. Experiment 2 tested two contrast levels but found no significant difference between them. Experiment 3 examined the effects of contrast in more detail while again fixing the phase shift at the optimal value of 90 degrees. Predictions from Equation 1 are straightforward. As the contrast of either or both of the frames increases, the ERD output increases. Any number of different contrast combinations, independent of their order and that have the same product, should produce the same output. For example, consider the products of the following arbitrarily chosen frame 1 and 2 contrast combinations: (.2)(.2) = .04, (.2)(.5) = .1, (.5)(.2) = .1, and (.5)(.5) = .25. From Equation 1, the first contrast combination will have the lowest ERD output. Discarding order, the second and third contrast pairs have the same ERD output and both are higher than the first but lower than the fourth pair. The contrast pairs can be ordered by their products or by another method, their ratios. The first and last pairs have 1:1 frame 1 to frame 2 contrast ratios, while the middle two have 1:2.5, irrespective of order. Based on contrast ratio, one might qualitatively predict that equivalent ratios would produce the same amount of bias and VMP. The ratio may be the relevant parameter not the contrast product.

Morgan and Cleary (1992) examined the effects of RDC contrast on $D_{MAX}$. They used four contrast combinations where the first and second frames were either low (0.1) or high (0.4) contrast. The ERD model predicts that the results should be ordered by their contrast products: low-low, low-high, high-low, and high-high (the two middle pairs being the same). Their predictions received less support than did predictions based on contrast ratio. They found that $D_{MAX}$ was greatest and nearly equivalent for both the low-low and high-high contrast conditions. Here, equal contrast ratios (1:1), irrespective of contrast product (0.01 versus 0.16), produced nearly identical levels of $D_{MAX}$ (about 4.5 arc minutes). The low-high and high-low contrast conditions caused comparable reductions in $D_{MAX}$, independent of presentation order. Their equal contrast products (0.04) did result in nearly equal $D_{MAX}$ values (about 2 arc minutes). The higher contrast ratio of 1:4 resulted in a lower $D_{MAX}$ than that of the lower 1:1 ratio.

It is not unusual for the visual system to use contrast ratio and to discard absolute luminance information. Hubel (1987) observed that when white paper with black print is viewed under indoor lighting, the white might be 12 units and the ink 0.6 units, which is a 20 to 1 contrast ratio where contrast equals the target intensity divided by the background intensity (Watson, 1986, p. 6-3). If viewed in bright outdoor lighting, the white could increase to 120 units and the ink to 6 units. The ratio is still 20:1 but the black and white areas are 10 times their original levels. Even though when viewed outdoors, the black actually exceeds the luminance of white when viewed indoors, black still appears to be quite black. Contrast ratio may be the critical piece of information, not contrast product or absolute luminance. This experiment was designed to disassociate contrast product effects from contrast ratio effects.

*Method*

Experiment 3 varied contrast among the 3 frames of the VMP sequence while holding other parameters constant. SW gratings of 1.4-cycle/degree, having a mean luminance of 4 $cd/m^2$, were viewed by the observer at 137 cm. Frame 1-2-3 durations were 1530-252-1530 ms, respectively. Frame phases for rightward and leftward VMP sequences were fixed at 0-270-90 degrees and 0-90-270 degrees, respectively. As previously noted, the priming signal arising from the frame 1 to 2 phase shift can be thought of as a biaser and the frame 2 to 3 counterphase shift as a probe. Hereafter, *biaser contrast ratio* refers to the ratio of frame 1 to frame 2 contrasts. *Probe contrast* is defined by the frame 2 and frame 3 contrasts. Experiment 3 varied the biaser contrast ratio over 6 values and held the probe contrast constant at either a low or high value. All of the contrast conditions are shown in Table 1. Frame 1 contrasts were 4, 6, 13, 19, 30, and 48% while frames 2-3 were either 19-19 or 48-48% contrast. Varying frame 1 contrast changed the ratio of the biaser signal. Presented in a randomized order, 6 frame 1 contrasts, at 2 probe contrasts, in 2 directions, with 10 repetitions each, yielded 240 stimuli for each of the 10 observers.

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Insert Table 1 about here

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*Results and Discussion*

Figure 12 shows Experiment 3 results, where VMP is plotted as a function of frame 1 contrast at both low and high frame 2-3 contrasts. Again, frame 1 contrast, relative to frames 2-3, which are fixed pairs of either 19-19% or 48-48% contrast, defines the biaser ratio and frame 2-3 contrasts form the probe.

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Insert Figure 12 about here

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An AxBxS within-subjects analysis of variance yielded the following results. As the biaser contrast ratio decreased, VMP significantly increased [$F(5,45) = 14.59$, $p = 0.0001$]; increasing the probe contrast had no significant effect [$F(1,9) = 4.78$, $p = 0.06$]; and the biaser by probe interaction effect was significant [$F(5,45) = 2.75$, $p = 0.03$].

When the biaser contrast ratio was highest, 4-48% contrast, VMP was the lowest at 82%. The largest biaser ratio for the lower 19% probe contrast condition, 4-19% contrast, was also low at 91.5% VMP. For both low and high contrast probe conditions, VMP quickly asymptoted to approximately the same level of 97% above 13% frame 1 contrast. Further increases in the biaser contrast caused a slight but nonsignificant downturn of the VMP curve.

The ERD model predicts a varied output as a function of both the products of the contrasts and the sine of the phase shift, for a 2-frame, SW grating presentation. In this experiment, the effect of priming phase shift is maximized by fixing it at 90 degrees. The contrast values of frames 1 and 2 can be in any order, any value, and the ERD output should be the same as long as their products are equal to a constant. Table 2 shows the biaser contrast product, contrast ratio, and mean percent VMP for each experimental condition to allow easier numeric comparisons. Inspection of

Insert Table 2 about here

the values in Table 2 and of the individual curves in Figure 12, show the predicted monotonic increase in mean percent VMP as frame 1 and 2 contrast product increases over low values within either the low or high contrast probe condition. However, the curves reveal a saturating nonlinearity which is not predicted by Equation 1. Also, when comparing the two curves before they asymptote, the mean percent VMP levels are reversed relative to their contrast products. Even though the low probe contrast condition held the overall biaser contrast products low, their VMP was higher than those in the high probe contrast condition.

Biaser contrast ratio appears to be a better predictor of VMP performance. The larger the biaser ratio, the more pronounced the decrement in VMP. Once the biaser ratio falls below 1:4, VMP asymptotes at a high value and there are no significant differences. The relative positions of the two curves are consistent with biaser ratio. The lower the contrast ratio, the higher was VMP. Direct comparisons can be made between contrast product and ratio. Referring to Table 2, compare the 6-19% to the 19-48% biaser contrast conditions. Their contrast ratios are about 1:3 and there is no significant difference between VMP performance [illegible] = -1.34, $p$ = 0.21], even though the contrast product differs by a factor of nine. Strength of priming did remain independent of frame order. There were no significant differences between the 19-48% and 48-19% contrast biaser ratio conditions [$t(9)$ = -1.18, $p$ = 0.27].

This study replicated the contrast results of Experiment 2. In that study, no significant differences in VMP were found for the 19% and 48% contrast conditions, which were 1:1 biaser ratios. Experiment 3 also found no significant differences [$t(9)$ = -0.54, $p$ = 0.60] for the 1:1 biaser ratios formed in the 19-19% and 48-48% contrast conditions.

The results of Experiment 3 replicate those found by Morgan and Cleary [illegible] where frame 1 to frame 2 contrast ratio was a better predictor of visual performance than contrast product. In both their study and in Experiment 3, observers' performance was less at the 1:4 contrast ratio than at the 1:1 contrast ratio. Independence of frame contrast order effects appeared to hold and was in complete agreement with the original prediction of the ERD model and Morgan and Cleary (1992). However, the independence is also consistent with contrast ratio predictions, and the latter provide a better overall explanation of the entire set of contrast results.

## EXPERIMENT 4: VISUAL MOTION PRIMING AND EYE MOVEMENTS

In order to discount eye movements as having an effect on the VMP phenomenon, a special, split-screen stimulus was constructed. The SW grating was divided at the center electronically. The right and left halves always jumped in opposite directions by using complementary phase sequences. For example, a 2-jump priming sequence for the right half would have the same sequence as used previously, 0-270-90 degree grating phases, while at the same time, the left half used 0-90-270 degree grating phases, creating outward VMP. The subject fixated the central display area and depending on the sequence, would simultaneously see both halves of the display priming either outwardly or inwardly. Since the eyes cannot simultaneously track motion in opposite directions, the VMP effect must be due to the motion signals arising from the phase changes between frames 1 and 2.

*Method*

The experimental trials combined the 3, 1-jump screening/practice sequences (outward, inward, and counterphase) with 3, 2-jump sequences; outward-counterphase and inward-counterphase for the priming conditions, plus a counterphase-counterphase sequence as a control. Before each stimulus presentation, the experimenter announced whether the next sequence would be either 1 or 2 jumps. The observer's response was one of the following six: out or in, for the 1-jump sequences and out/out, out/in, in/out, or in/in, for the 2-jump sequences. The spatial frequency conditions were 1.4 and 2.8 cycles/degree. All SW gratings were 19% contrast. The 6 different jump sequences were randomized within a given spatial frequency block, and presented in a counterbalanced order among the observers. The 4 cd/m$^2$ gratings were viewed at a 137 cm distance. Six different jump sequences, at 2 spatial frequencies, with 10 repetitions yielded 120 stimuli presented to each of the 5 observers.

*Results and Discussion*

Using either 1.4- or 2.8-cycle/degree SW gratings had no effect on the perception of either outward or inward VMP; thus the results shown are collapsed across spatial frequency. The mean percentage of different categories of perceived motion for single-jump presentations are shown in Figure 13. Outward and inward

Insert Figure 13 about here

split-field presentations were seen to move in the same direction as that physically presented, 99 and 100% of the time, respectively. Single-jump counterphase presentations were seen to move at near chance levels of 55% outward and 45% inward. The results of the 2-jump priming sequences are shown in Figures 14 and 15. Observers saw split-field priming 89% of the time for the outward and 96% for

Insert Figures 14 & 15 about here

the inward direction. Since an observer's eyes cannot simultaneously track objects moving in opposite directions, these results confirm that the VMP phenomenon is not due to eye movements. As a check, observers were also shown 2-jump, counterphase sequences. There were four possible kinds of observations, out/out, in/in, out/in, and in/out. The results were 30, 9, 26, 35% for the 4 categories of motion (see Figure 16). These responses are close to the 25% level expected if each jump were perceived randomly as in or out.

Insert Figure 16 about here

## GENERAL DISCUSSION

### *Overview*

When a SW grating is abruptly phase shifted 90 degrees, an observer sees it move unambiguously in the 90-degree direction. Presumably, one motion directional subunit responds more strongly than its counterpart. The signal persists for a finite period of time. Conversely, in isolation, a 180-degree shift of a SW grating is seen as ambiguous motion where neither left nor right directions predominate. Supposedly, leftward and rightward motion subunits respond equally. If a 90-degree phase shift of a SW grating precedes a 180-degree shift, the persistent motion energy produced from the first signal is integrated with that of the second. Visual motion priming occurs when the residual bias serves to disambiguate the motion of the second counterphase grating, in the same direction as that physically presented by the first grating.

Earlier studies (Anstis & Ramachandran, 1987; Eggleston, 1984; Ramachandran & Anstis, 1983) relied on dot sequences to bias the perception of bistable figures. Their findings led to the concept of visual inertia or momentum. Unfortunately, the complexity of dot spatial frequency spectra makes it difficult to apply their results to motion-from-Fourier-components models. The present experiments on VMP are unique because they use (but are not restricted to) SW gratings in a biasing (priming) paradigm. Sine-wave characteristics such as spatial frequency, contrast, and phase are more easily manipulated than those of dot stimuli. This more readily allows evaluation of the predictions of formal motion models.

VMP was first described as being analogous to biasing the perception of bistable dot figures. Several related studies (McKee & Welch, 1985; Nakayama & Silverman, 1984; Snowden & Braddick, 1989) were also reviewed with the general finding that the combination of motion signals over small enough spans of time was due to physiological, not probability summation. In their study, McKee and Welch

(1985) examined the effects of varying the number of line elements presented in an apparent-motion sequence. Since an observer was required to report the direction of motion of a sequence of stimuli as a group, the effects of multiple motion steps could have been due to probability summation. McKee and Welch (1985) had to perform several control studies to enable them to rule out probability summation in favor of physiological summation. By comparison, VMP is different in that an observer's judgment is about the direction of motion of one jump in a sequence, not about the sequence as a whole. Even though VMP involves the presentation of two motion signals, the priming effect is based solely on the perceived direction of the counterphase SW grating. An observer has no multiple chances of seeing the direction of motion of the counterphase jump. In addition, the results of McKee and Welch (1985) may have been confounded by position cues. Later positions of a line are different from earlier positions, and an observer can simply compare positions to infer motion direction. In VMP, an observer responded to a single counterphase jump of a SW grating. An observer could not determine direction of motion by comparing the position of the grating after the jump with its position before the jump.

*The Nature of Visual Motion Priming*

In order to fully understand the nature of VMP, a detailed look will now be made of how motion signals are processed at the different stages within an ERD model (refer to Figure 6). In this implementation of the model, there are spatial and temporal filters after the receptors. The spatial filter impulse responses are even- and odd-symmetric Gabor functions. The even-symmetric Gabor filter is a cosine function centered in a Gaussian window and the odd-symmetric filter is a sine function centered in a Gaussian window. The impulse responses of the two types of temporal filters have different durations and are biphasic where there is first an excitatory phase followed by an inhibitory phase. The filtered signals are then multiplied. These elements and stages are simply adopted from models like that of van Santen and Sperling (1984). At this point in the signal processing, the persistence of individual leftward and rightward motion signals is not long enough to account for the results of Experiment 2 because they are the outputs of the spatiotemporal filters that persist for only 30 to 50 ms (Bergen & Wilson, 1985; van Santen & Sperling, 1984) whereas VMP occurred over a 190 to 770 ms range. Some form of filter is needed to lengthen the relatively short duration directional signals. To increase persistence, filters could be placed after the multiplication stages. The standard ERD model utilizes infinite-time averaging integration filters in each directional pathway to remove time-dependent components. Infinite-time averaging is a mathematical device that allows the model to function properly, but was never meant to suggest that motion signals are combined over infinitely long time periods. The amount of temporal integration required to account for the VMP findings is neither zero nor infinite. One possible method to improve the model is to replace the temporal integration filter with one that has a Gaussian impulse response, as described by Equation 3 (Bergen & Wilson, 1985) and plotted in

$$y = t^{s}\exp^{-d \cdot t}. \qquad \text{Equation 3}$$

Figure 17. In the expression describing the filter response, y is the output, t is time, and s and d are parameters that determine the steepness and decay of the output. This filter is convolved (or multiplied in the Fourier domain) with the outputs of the multiplicative stages and acts to lengthen the persistence of the

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Insert Figure 17 about here

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directional subunit responses. The Gaussian filter can be designed to produce signals that are in the 100's of millisecond range to explain the duration results of Experiment 2 (see Figure 11). The leftward and rightward subunit activity levels are compared by subtraction. This resultant output represents the opponent energy where positive and negative values indicate leftward and rightward motion, respectively, and the opponent output will have a persistence that corresponds to the persistence of the directional signals from which it was derived.

Merely extending the directional-subunit responses via integration filters and then examining the opponent-energy output may provide an adequate explanation for the priming phenomenon but it creates other difficulties. In order to understand why, a detailed look at subunit directional signals and the opponent signal is required. Figure 18 illustrates the effects of varying Frame 2 duration and changing the location of the Gaussian temporal integration filter on the signal processing of VMP by the ERD. Figure 18a depicts both the individual leftward and rightward selective subunit activities (top) as well as their subtracted, opponent-energy output (bottom), plotted as a function of time. At the instant of a leftward priming

Insert Figure 18 about here

signal (the frame 1 to frame 2 transition or F1-F2), both leftward and rightward subunit activity increases but the leftward response is more vigorous. The responses immediately begin to decay in accordance with the early spatiotemporal filter stage characteristics and the Gaussian filters placed after the multiplicative stages. For a long frame 2 duration (> 500 ms) the subunit activities return to zero before the occurrence of the counterphase jump (F2-F3 transition). When the counterphase occurs at the F2-F3 transition, the left and right subunits respond equally. There is no leftover subunit activity from the F1-F2 transition to be added to that produced by the F2-F3 jump. The corresponding opponent output shows a decaying leftward imbalance in response to the priming signal which returns to zero imbalance (the dotted threshold line) before the F2-F3 transition. There is no opponent response to the counterphase signal. Since there is no residual bias at the instant of the counterphase signal, no VMP effect is observed.

In Figure 18b, the time between the priming and counterphase signals is reduced (frame 2 duration < 500 ms). The subunit directional signals do not return to zero before the presentation of the counterphase jump of the SW grating. When the counterphase jump occurs at the F2-F3 transition, an equivalent increase in subunit activity is added to each subunit directional signal. Left and right activity levels increase, but the net difference between them remains the same as that just before the F2-F3 transition. Throughout the entire VMP sequence, the ERD's opponent-energy output decays towards threshold. The residual-opponent energy remains unchanged at the instant of the 180-degree shift of the SW grating. The indication of a temporal event by increased subunit activity, coincident with a residual opponent-energy imbalance, results in the counterphase signal being perceived as moving in the same direction as the priming signal. The extent to which the counterphase signal is disambiguated (VMP) indicates the amount of residual opponent-motion energy.

Figure 18b depicts a model that explains VMP and can account for the frame 2 duration results of Experiment 2. Placing Gaussian temporal integration filters after the multiplicative stages serves to extend the time course of the short-duration subunit impulse responses as well as the opponent-energy output.

At this point, it seems important to make the distinction between non-directional and directional temporal events. Presumably, non-directional events would depend on the functional characteristics of subunit activity and directional events would depend on the opponent-output activity because only the opponent signal explicitly compares two directions. It is known that the visual system responds to short-duration non-directional events at rates up to 30-60 Hz which reflects an impulse response duration of 10's of milliseconds.. Conversely, Experiment 2 results require an extended temporal integration period to account for VMP. Therefore, subunit activity and opponent signals in the model would seem to require different time courses. Short non-directional temporal signals and long directional signals need to be separated in a better model.

Since the temporal filter and subtractive stages are linear operators, their order can be changed to that shown in Figure 19 without affecting the characteristics of the opponent signals. In this new arrangement, the short-duration subunit outputs go directly to the subtraction stage, followed by a temporal integration stage that has a Gaussian impulse response. This allows the subunit responses to remain short to detect fast temporal events. Only the opponent-energy persistence has been lengthened to facilitate the combination of opponent motion signals over time.

---

Insert Figure 19 about here

---

For a relatively short frame 2 duration (< 500 ms), Figure 18c shows the directional-subunit and opponent-energy activity in response to a VMP sequence when the Gaussian temporal integration filter is placed after the subtraction stage. After the priming signal, there are short-duration, subunit imbalances that quickly decay and return to zero. Note that their responses are much shorter than those shown in Figures 18a and 18b. The corresponding opponent-energy output also returns to threshold but at a much slower rate than the subunits because of the location and the impulse response characteristics of the temporal integration filter. At the instant of the F2-F3 transition, the directional-subunits respond equally. The equivalent elevation in activity of both subunits could signal that another temporal event has occurred, but with an unknown direction. A check of the extended opponent-energy output, however, reveals that a leftward bias remains. The residual leftward imbalance, at the time of the counterphase signal, causes the observer's perception to be disambiguated and the jump appears to move in the same direction as the priming signal. The degree to which the perceived direction of the counterphase signal (the probe) is disambiguated by the priming signal (the biaser) reflects the amount of residual opponent energy.

*Summary of Results and the Elaborated Reichardt Detector Model*

The results of this series of studies forms the first comprehensive look at the spatiotemporal aspects of the VMP phenomenon. Experiment 1 examined the effects of varying the frame 1 to frame 2 phase shift on VMP. An analytic derivation by van Santen and Sperling (1985) made the prediction that priming strength would vary directly with the sine of the SW grating phase shift. The results revealed an inverted U-shaped curve that had its peak at 90 degrees and which exhibited a high degree of fit to a sine function. A maximum response to a 90-degree phase-shifted SW grating is a general prediction of motion models that use spatial filters in quadrature phase (van Santen & Sperling, 1984, 1985; Watson, 1990). The Experiment 1 VMP phase-shift data supported the model.

The ERD, as originally formulated by van Santen and Sperling (1984, 1985), utilized an infinite-time averaging filter after the multiplication stage in order to eliminate time-varying components. However, it is not practical to combine motion signals over an infinite time period. In Experiment 2, VMP occurred over a 190 to 770 ms range. The model can account for these results by changing the temporal integrator to a Gaussian bandpass filter and placing it after the subtraction stage.

Experiment 2 used 0.7-, 1.4-, and 2.8-cycle/degree SW gratings. Increasing spatial frequency significantly lowered mean percent VMP. This trend parallels the results of Lovegrove and Meyer (1984) who found that for statically presented square-wave gratings, visual persistence decreased over a 2- to 4-cycle/degree range.

Two levels of contrast were also tested, but no significant differences were found. From Equation 1, different contrast products should have produced different VMP performance. The results did not support the ERD model and warranted further investigation into the effects of contrast.

The ERD model predicts that the opponent output is a function of the product of frame 1 and frame 2 contrasts times the sine of their phase shift, independent of their order. Experiment 3 varied the biaser and probe contrasts while holding the priming phase shift at the optimal value of 90 degrees. No differences were found due to frame contrast order. If the data were examined within either the low or the high probe contrast condition, then as the biaser contrast product increased so did VMP. This increase is predicted by Equation 1. Contrast product was found to be a poor predictor of VMP strength when compared across the two probe conditions. In fact, results were opposite to those predicted by the contrast product. The VMP data also exhibited asymptotic behavior as biaser contrast was manipulated, a finding which is not consistent with the ERD model. The ratio formed between the frame 1 and frame 2 contrasts was a better predictor of VMP performance. Relatively high biaser contrast ratios (above 1:4) caused larger decreases in VMP. For biaser contrast ratios below 1:4, priming performance asymptoted above 95%. These results replicated the basic findings of Morgan and Cleary (1992) using a different paradigm, but are not predicted by the standard ERD model.

In order to discount eye-movement artifacts, a special split-screen presentation was shown to observers. They spontaneously saw either outward or inward VMP. Since the eyes cannot track motion in opposite directions, it was concluded that VMP was not due to eye movement.

*Future Research*

Experiment 2 demonstrated that VMP significantly decreased as spatial frequency was increased from 0.7 to 2.8 cycles/degree. Even though this parallels static grating results found by Lovegrove and Meyer (1984), it is still unclear what kind of mechanism may account for this type of finding.

The effects of priming contrast ratio found in Experiment 3 indicate that the motion system must be incorporating some form of automatic gain control that seems to act quickly to normalize contrast with respect to the higher contrast frame. The predicted lack of contrast order effects was verified, further complicating a solution. Take for example, a priming signal that is composed of a low contrast frame followed by a high contrast frame. The mechanism might normalize to the higher value but it would also have to adjust its initial response to the first frame, which occurred in isolation, before the presentation of frame 2. Such a mechanism might be a fast automatic gain control with some form of feedback loop.

The luminance-domain stimuli used in these experiments, reflect the behavior of first-order motion mechanisms. It would be interesting to know whether the priming properties of second-order mechanisms (Cavanagh & Mather, 1989; Chubb & Sperling, 1989; Petersik, 1989), as revealed by prior experiments with non-luminance domain stimuli, would be similar to first-order motion mechanisms.

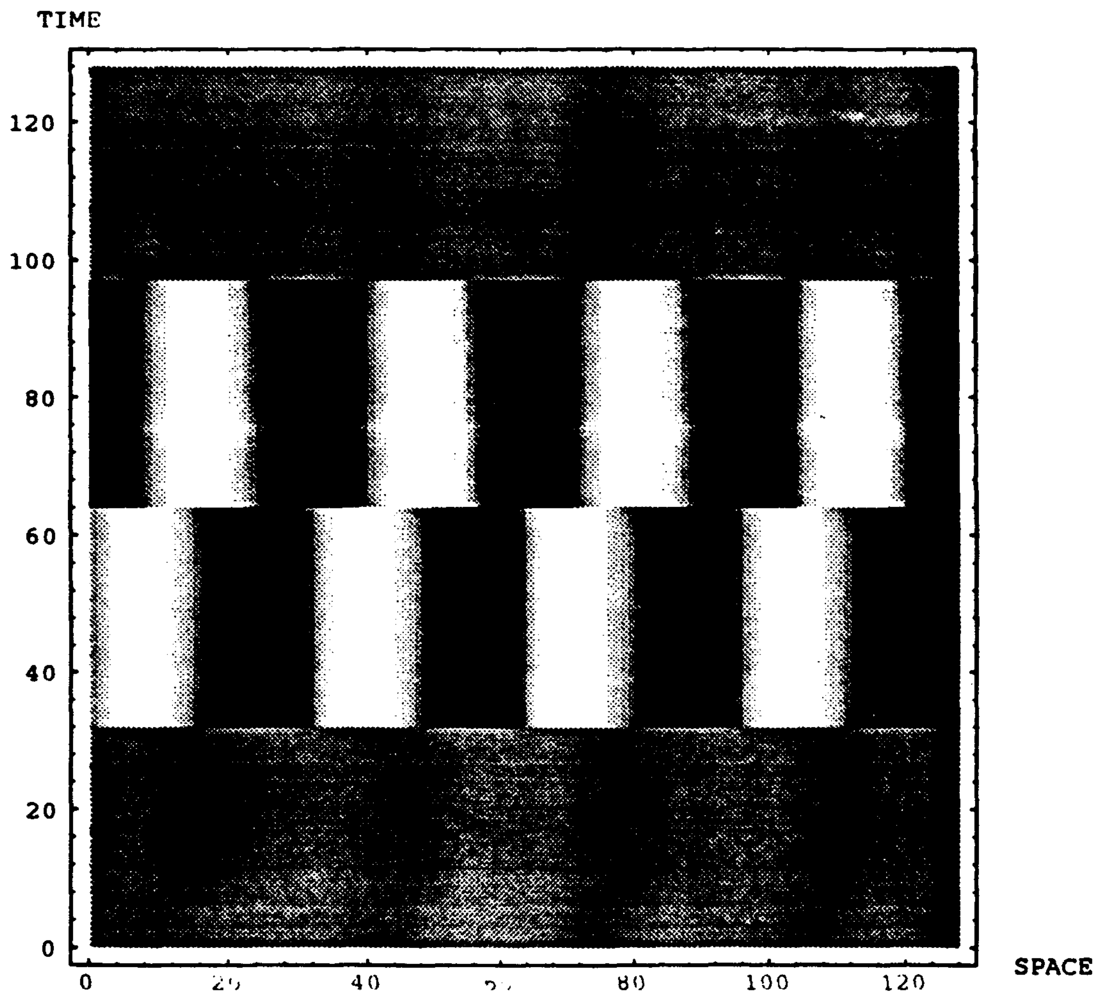
Table 1. Independent variable combinations of biaser contrast ratio (frames 1-2) and probe contrast (frames 2-3) used in Experiment 3.

| 19% Contrast Probe | 48% Contrast Probe |
|---|---|
| Frames 1-2-3 | Frames 1-2-3 |
| 4-19-19 | 4-48-48 |
| 6-19-19 | 6-48-48 |
| 13-19-19 | 13-48-48 |
| 19-19-19 | 19-48-48 |
| 30-19-19 | 30-48-48 |
| 48-19-19 | 48-48-48 |

Table 2. Mean percent visual motion priming results of Experiment 3, compared to their corresponding contrast product and contrast ratio values, at each level of biaser contrast ratio (frames 1-2) and under two probe contrast conditions (frames 2-3).

| 19% Contrast Probe | | | | 48% Contrast Probe | | | |
|---|---|---|---|---|---|---|---|
| Biaser Contrast | Product | Ratio | Mean %VMP | Biaser Contrast | Product | Ratio | Mean %VMP |
| 4-19 | .008 | 1:5 | 91.5 | 4-48 | .019 | 1:12 | 82 |
| 6-19 | .011 | 1:3 | 95 | 6-48 | .029 | 1:8 | 92 |
| 13-19 | .025 | 1:1.5 | 96.5 | 13-48 | .062 | 1:3.7 | 95.5 |
| 19-19 | .036 | 1:1 | 97 | 19-48 | .091 | 1:2.5 | 97.5 |
| 30-19 | .057 | 1.6:1 | 96.5 | 30-48 | .144 | 1:1.6 | 97.5 |
| 48-19 | .091 | 2.5:1 | 95.5 | 48-48 | .230 | 1:1 | 95.5 |

Figure 1. Space-time plot of a 4-cycle/degree sine-wave grating abruptly phase shifted 90 degrees to the right.



TIME
120
100
80
60
40
20
0
0
40
80
100
120
SPACE

Figure 2. Space-time plot of a 4-cycle/degree sine-wave grating abruptly phase shifted 180 degrees.

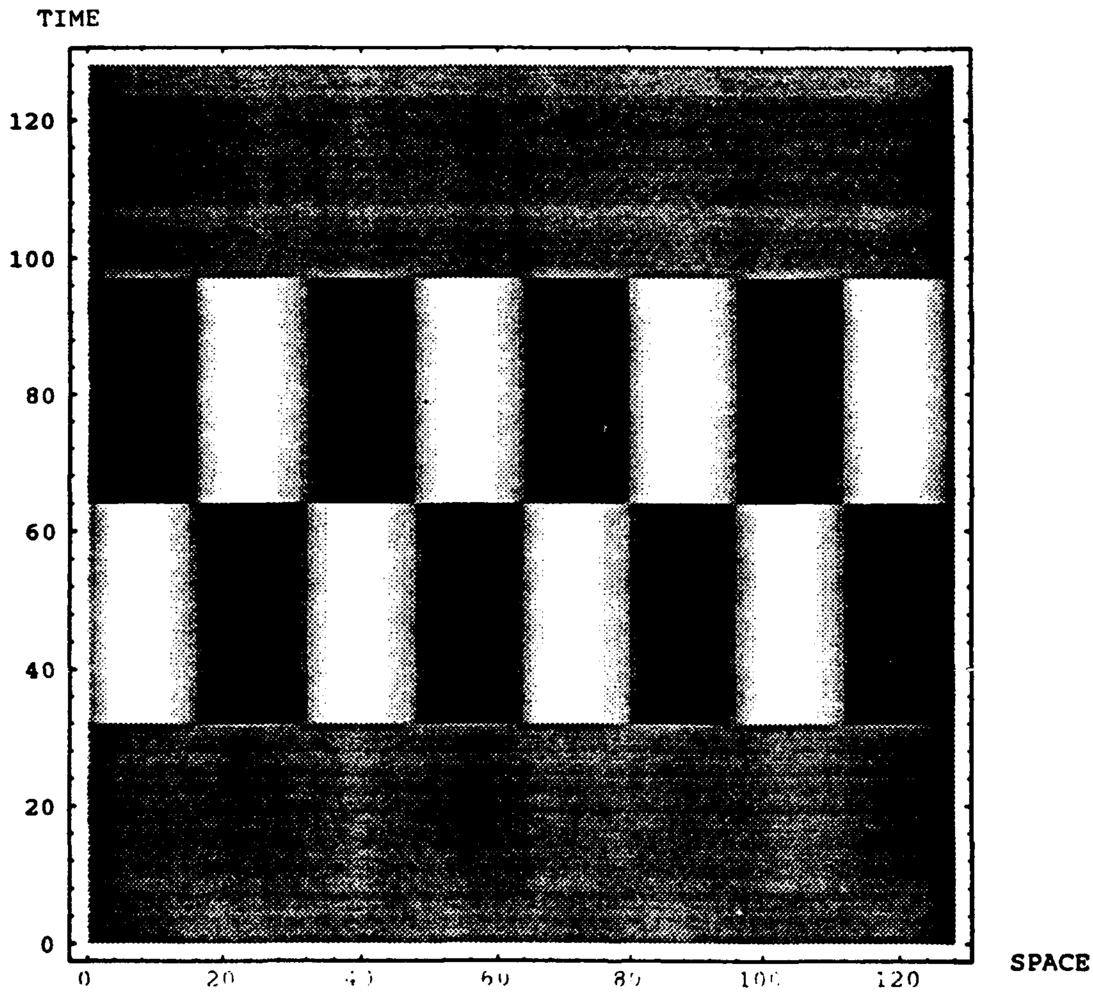

TIME
120
100
80
60
40
20
0
0
20
40
60
80
100
120
SPACE

Figure 3. Space-time plot of a rightward visual motion priming sequence, where a stationary 4-cycle/degree sine-wave grating is abruptly phase shifted rightward 90 degrees, then followed by a 180-degree phase shift (from Pantle, Pinkus, & Strout, 1992).

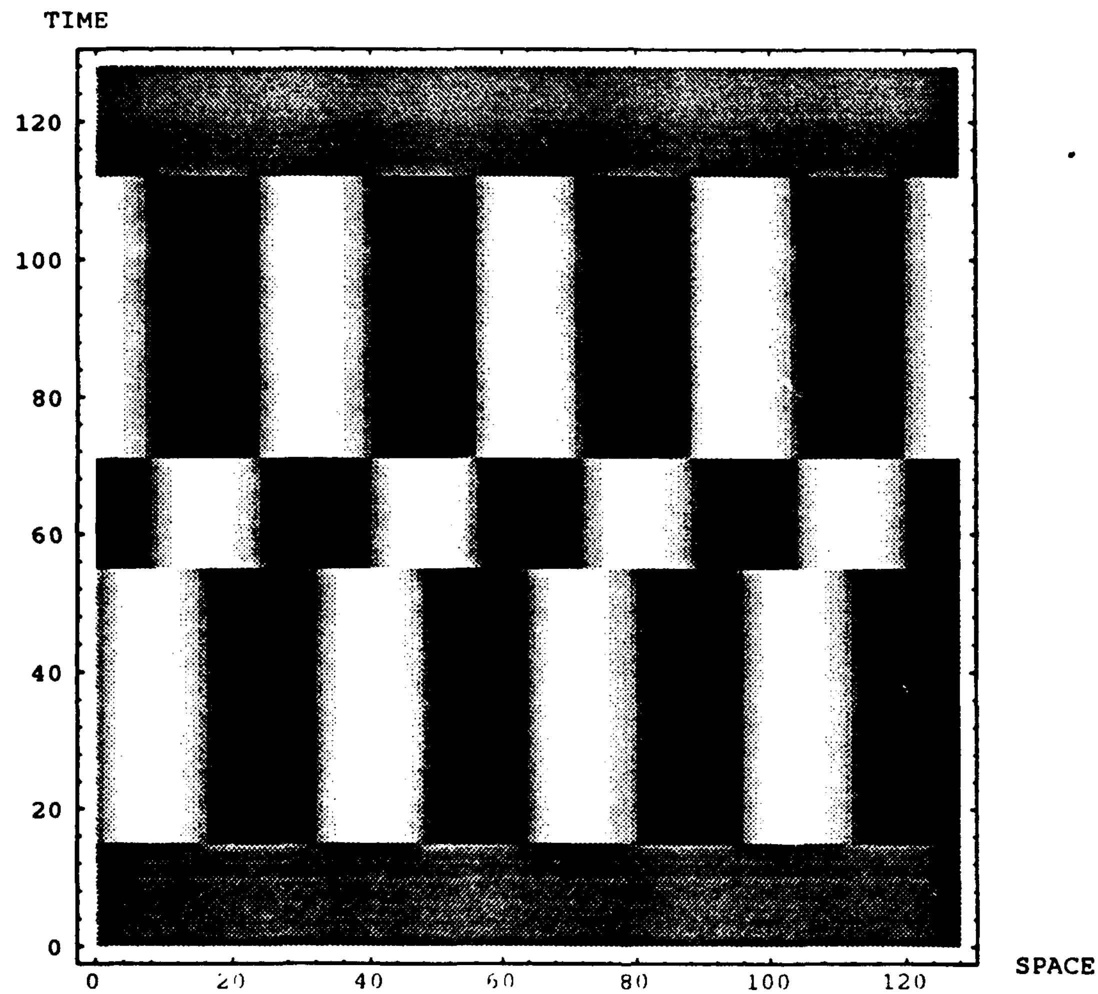

TIME
120
100
80
60
40
20
0
0
20
40
60
80
100
120
SPACE

Figure 4. (a) Four-dot, bistable diamond, apparent motion figure (after Ramachandran & Anstis, 1983).

(b) "Streaming" and "bouncing" percepts of apparent motion dot sequences (after Ramachandran & Anstis, 1983).

(c) Priming dots for a bistable diamond (after Anstis & Ramachandran, 1987).

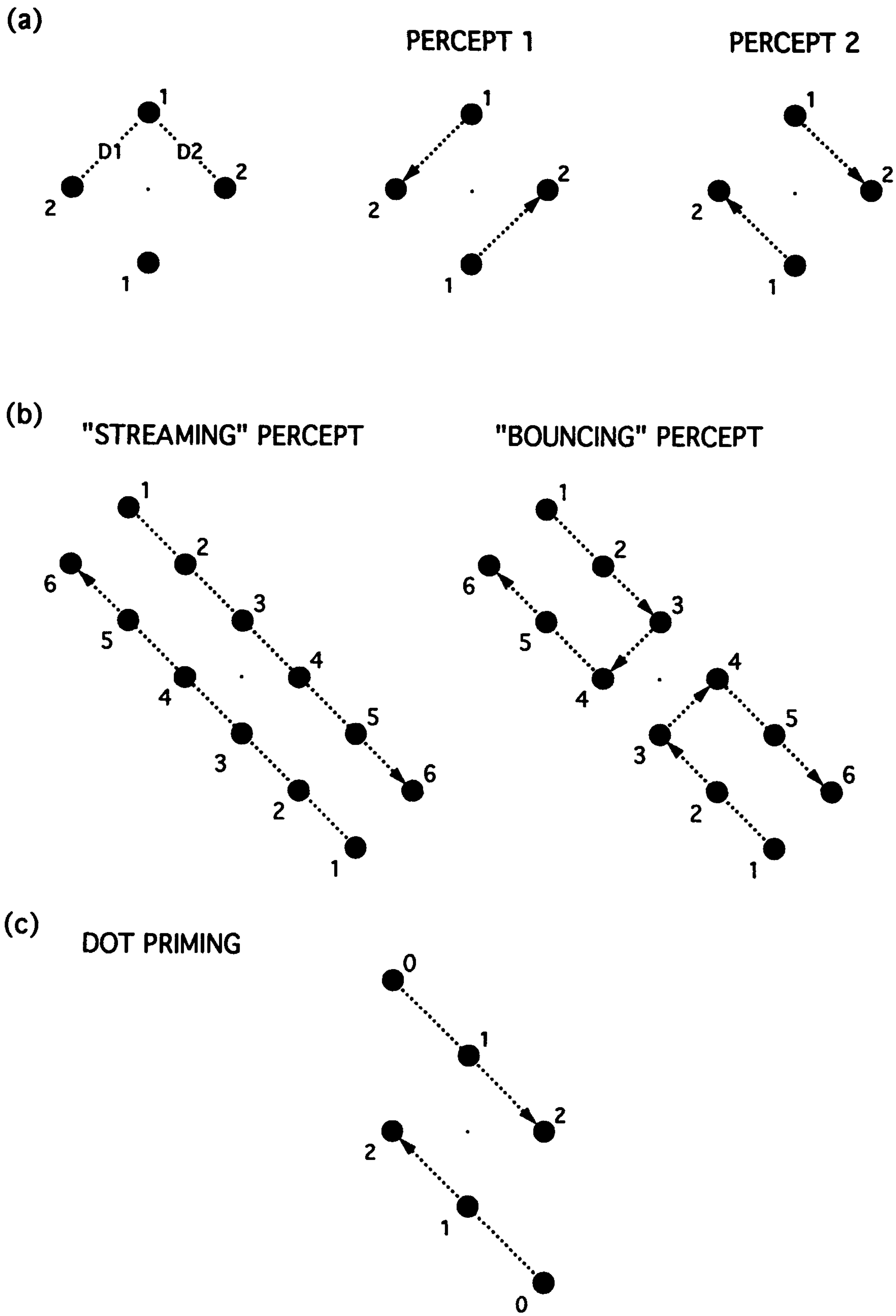

(a)
PERCEPT 1
PERCEPT 2
D1
D2
(b)
"STREAMING" PERCEPT
"BOUNCING" PERCEPT
(c)
DOT PRIMING

Figure 5. The Reichardt model of motion detection (after van Santen & Sperling, 1984).

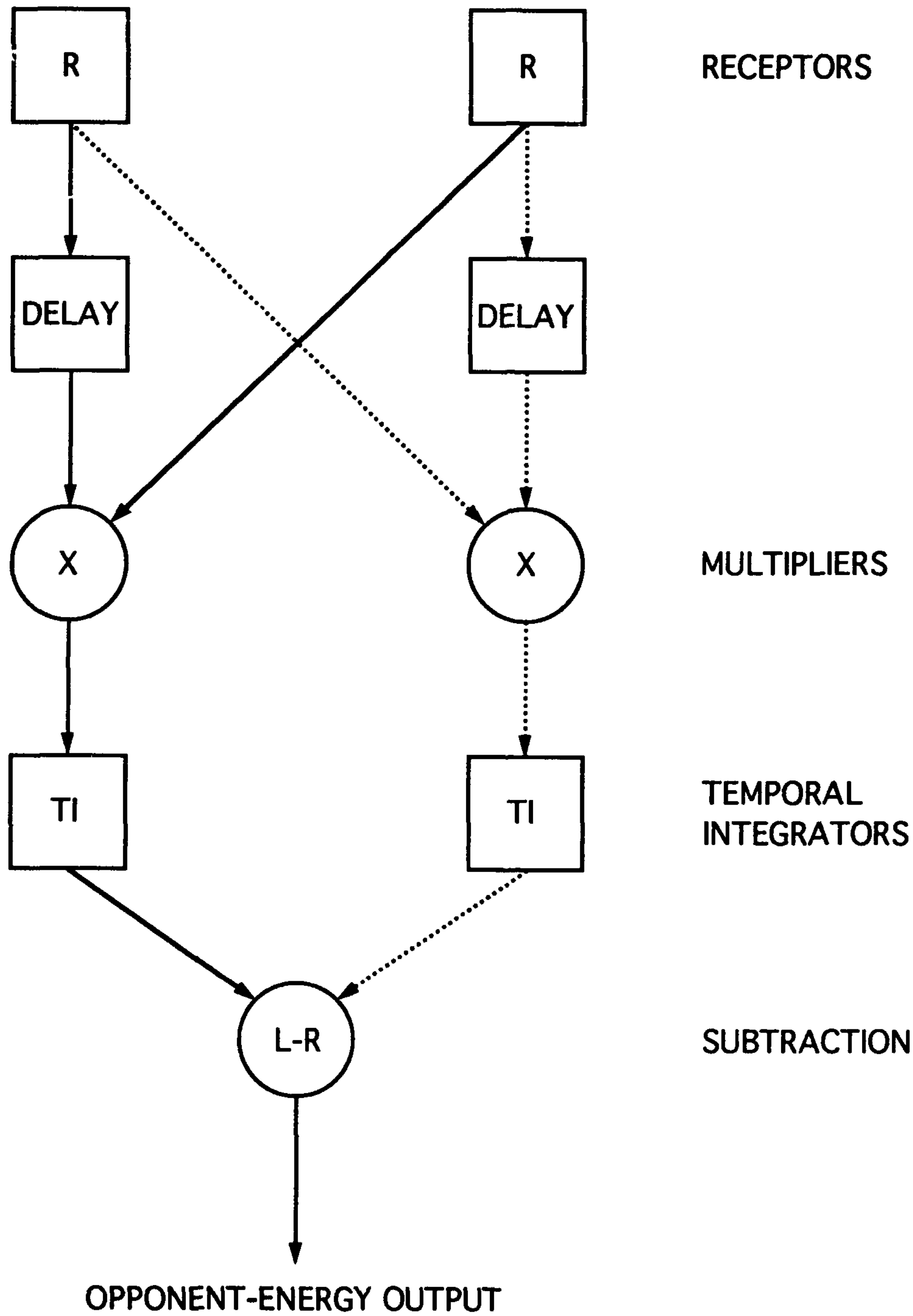

R
R
RECEPTORS
DELAY
DELAY
X
X
MULTIPLIERS
TI
TI
TEMPORAL
INTEGRATORS
L-R
SUBTRACTION
OPPONENT-ENERGY OUTPUT

Figure 6. The elaborated Reichardt detector model (after van Santen & Sperling, 1984, 1985).

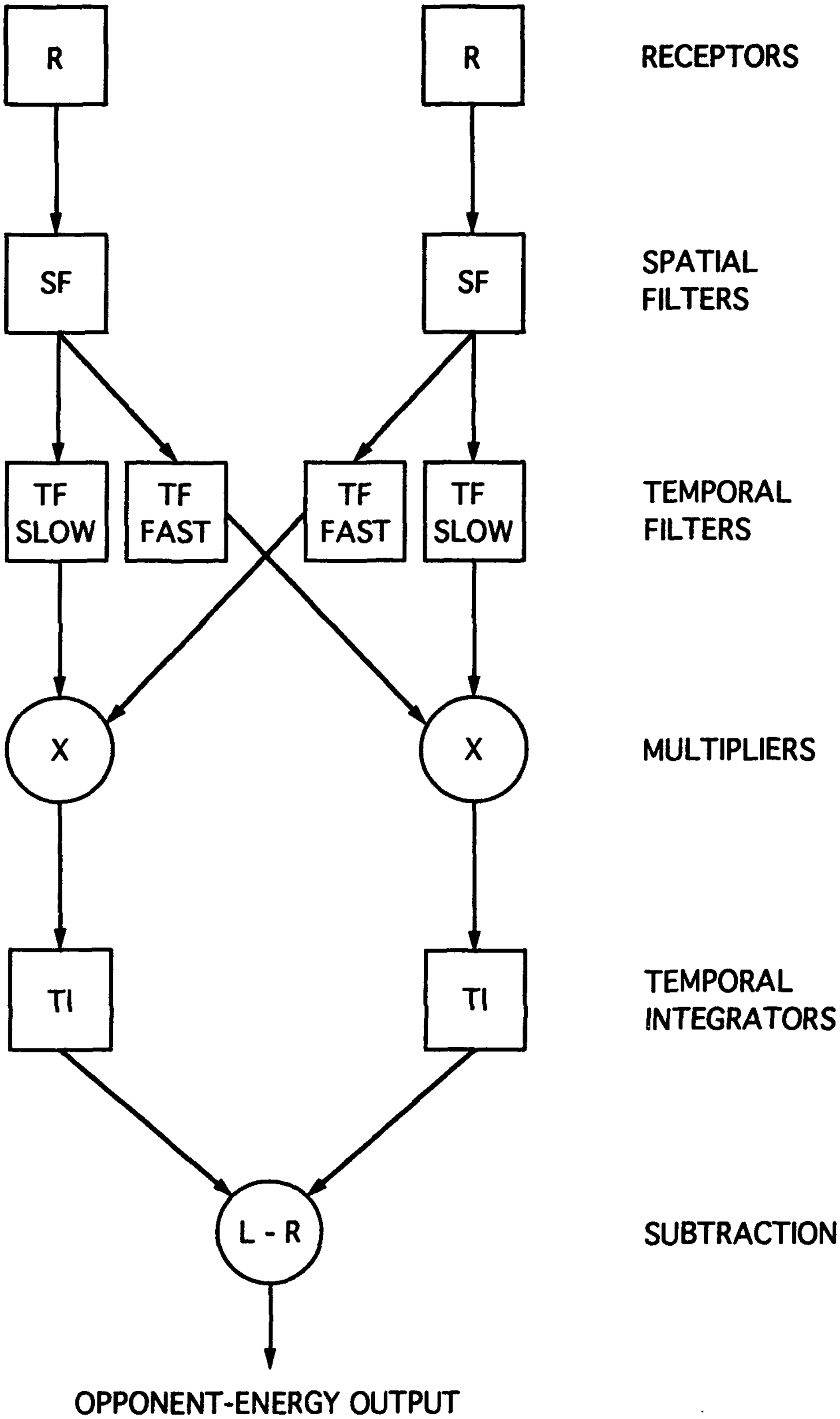

R
R
RECEPTORS
SF
SF
SPATIAL
FILTERS
TF
SLOW
TF
FAST
TF
FAST
TF
SLOW
TEMPORAL
FILTERS
X
X
MULTIPLIERS
TI
TI
TEMPORAL
INTEGRATORS
L - R
SUBTRACTION
OPPONENT-ENERGY OUTPUT

Figure 7. Mean percent visual motion priming (VMP) as a function of frame 1 to frame 2 phase-shift magnitude.

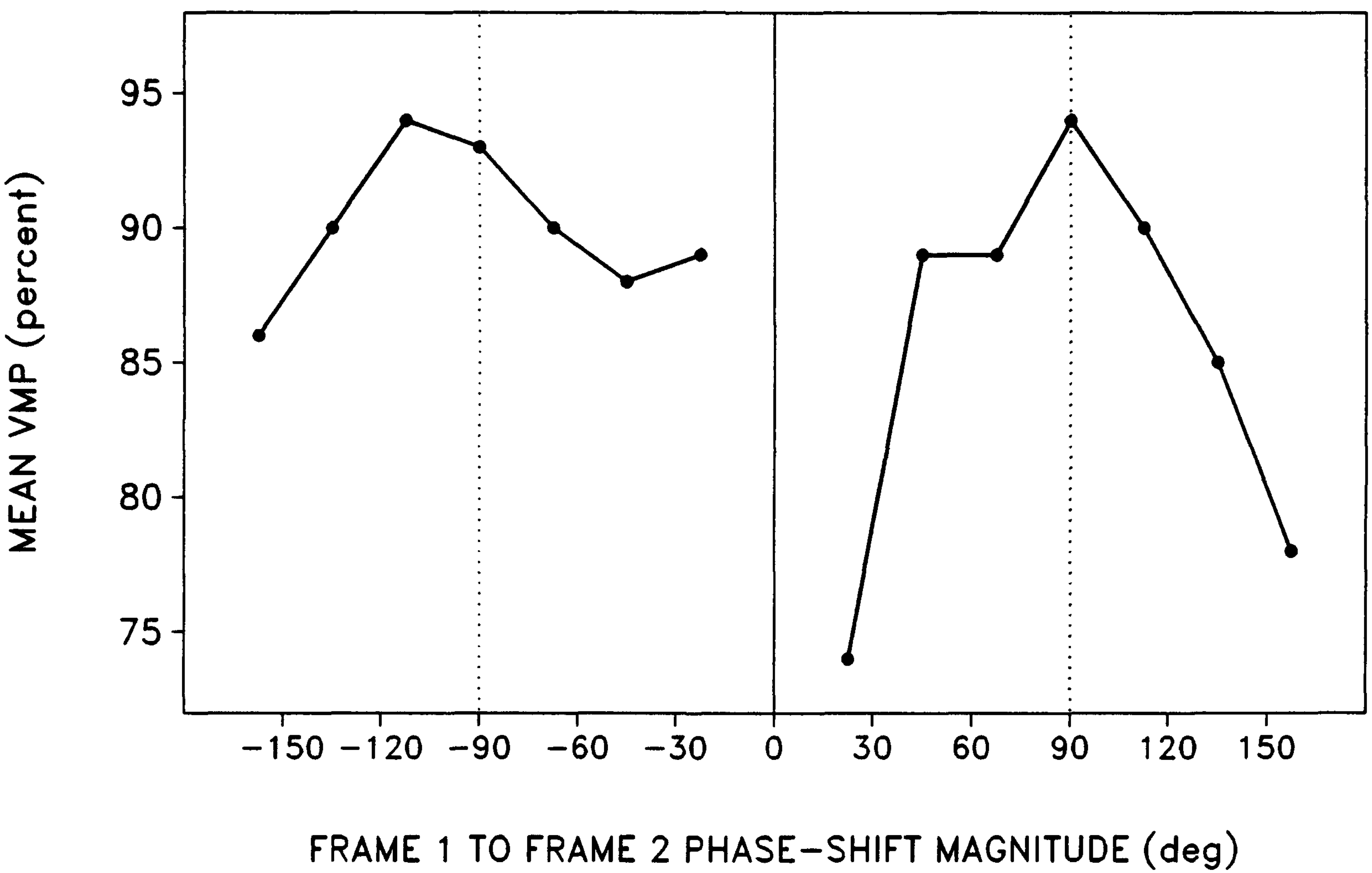
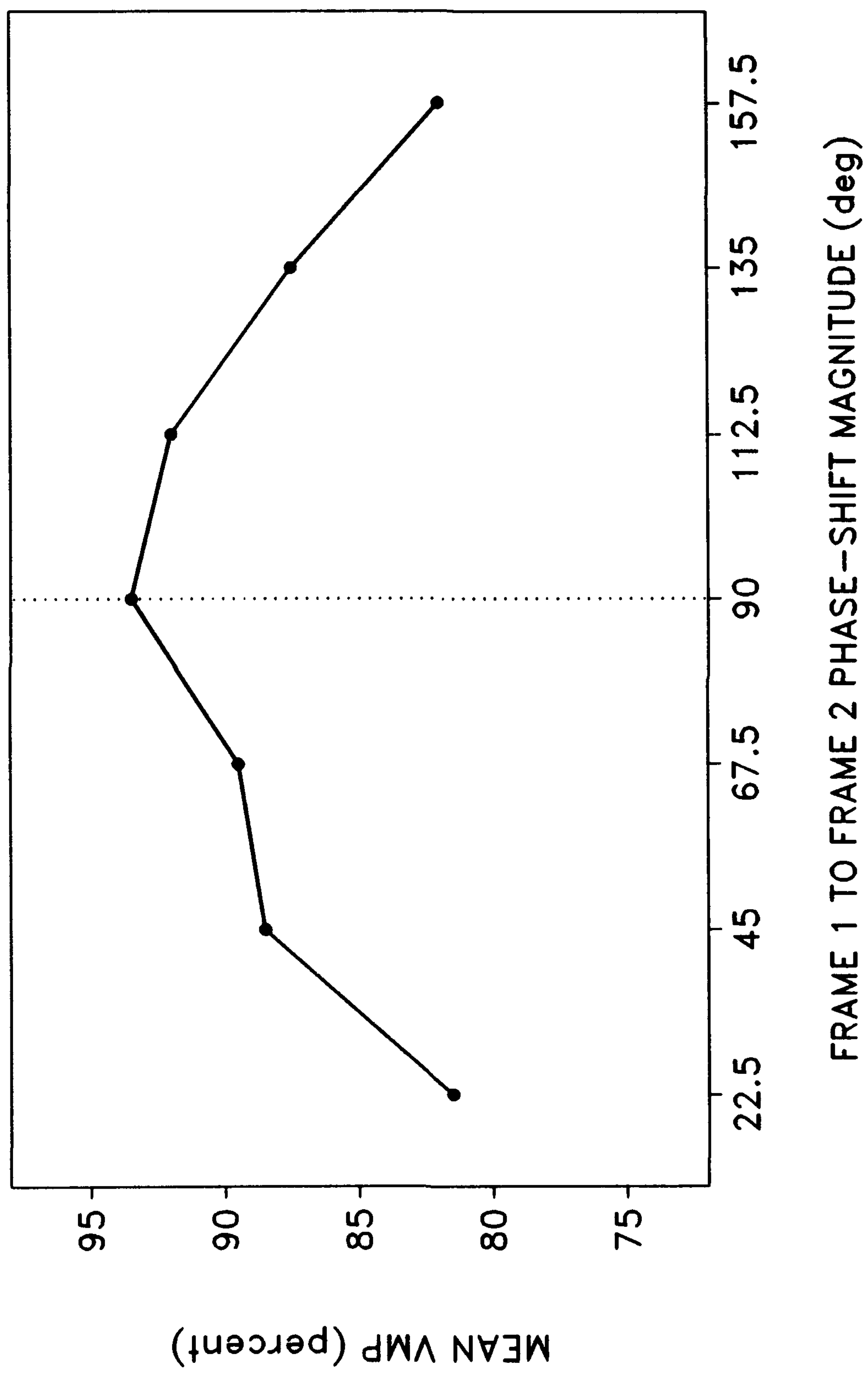

95
90
85
80
75
MEAN VMP (percent)
−150 −120 −90 −60 −30 0 30 60 90 120 150
FRAME 1 TO FRAME 2 PHASE−SHIFT MAGNITUDE (deg)

Figure 8. Mean percent visual motion priming (VMP) as a function of frame 1 to frame 2 phase-shift magnitude collapsed across direction.



MEAN VMP (percent)
95
90
85
80
75
22.5
45
67.5
90
112.5
135
157.5
FRAME 1 TO FRAME 2 PHASE-SHIFT MAGNITUDE (deg)

Figure 9. Predicted (solid line) and measured (dots) mean percent visual motion priming (VMP) as a function of frame 1 to frame 2 phase-shift magnitude.

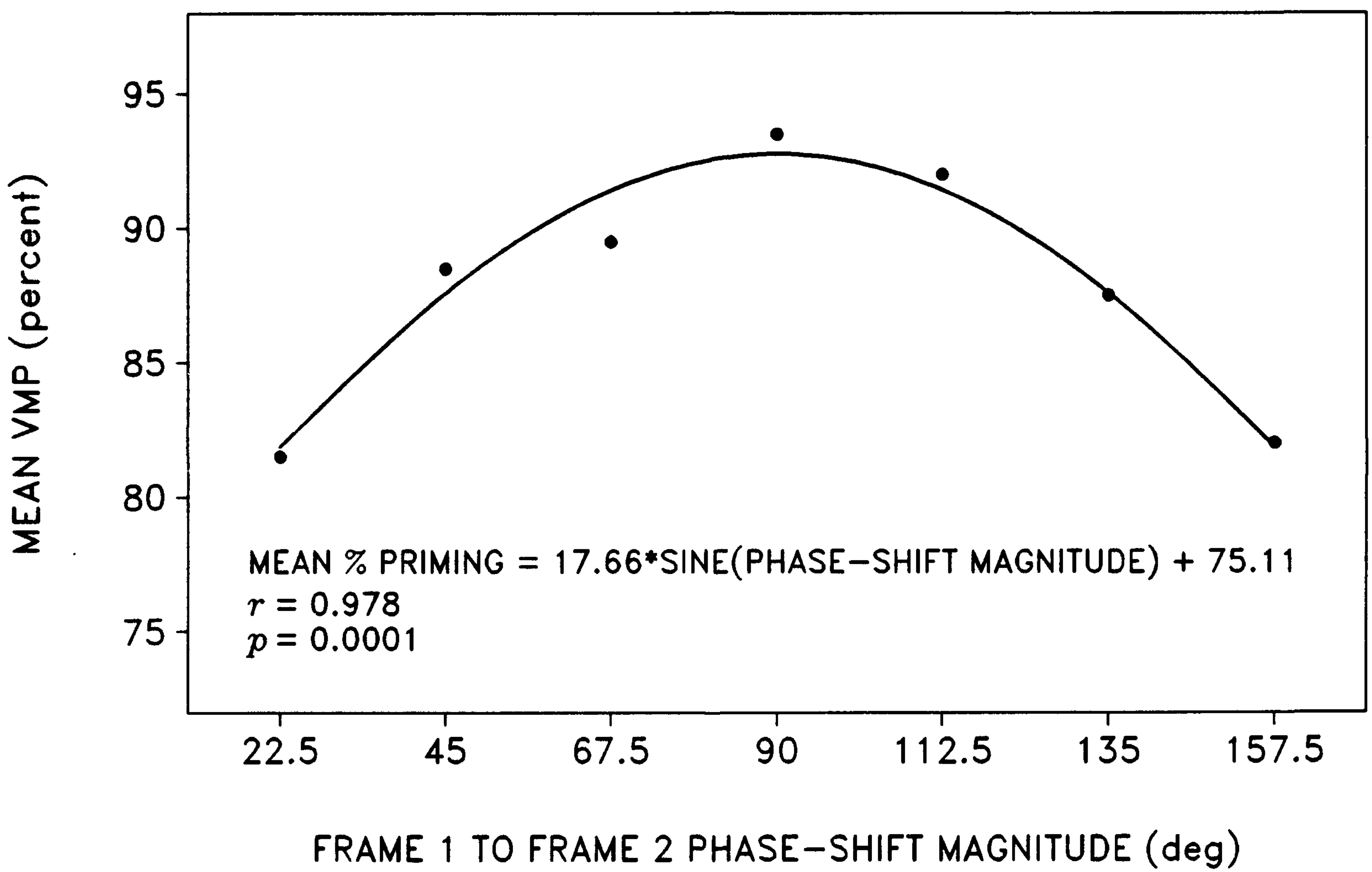
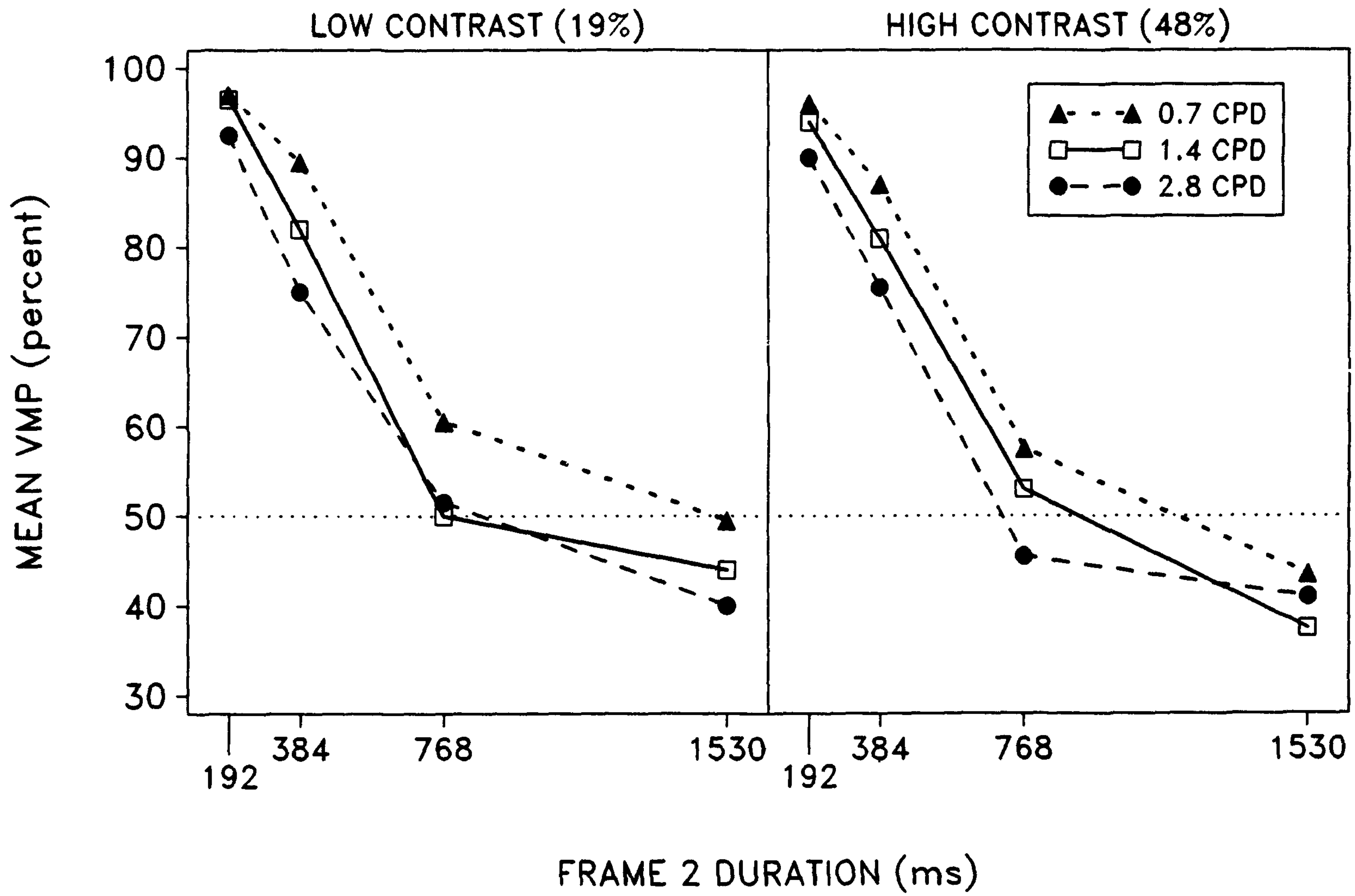

95
90
85
80
75
MEAN VMP (percent)
MEAN % PRIMING = 17.66*SINE(PHASE–SHIFT MAGNITUDE) + 75.11
r = 0.978
p = 0.0001
22.5
45
67.5
90
112.5
135
157.5
FRAME 1 TO FRAME 2 PHASE–SHIFT MAGNITUDE (deg)

Figure 10. Mean percent visual motion priming (VMP) as a function of frame 2 duration, spatial frequency, and contrast.



LOW CONTRAST (19%)
HIGH CONTRAST (48%)
MEAN VMP (percent)
100
90
80
70
60
50
40
30
192
384
768
1530
0.7 CPD
1.4 CPD
2.8 CPD
FRAME 2 DURATION (ms)

Figure 11. Mean percent visual motion priming (VMP) as a function of frame 2 duration and spatial frequency, collapsed across contrast.

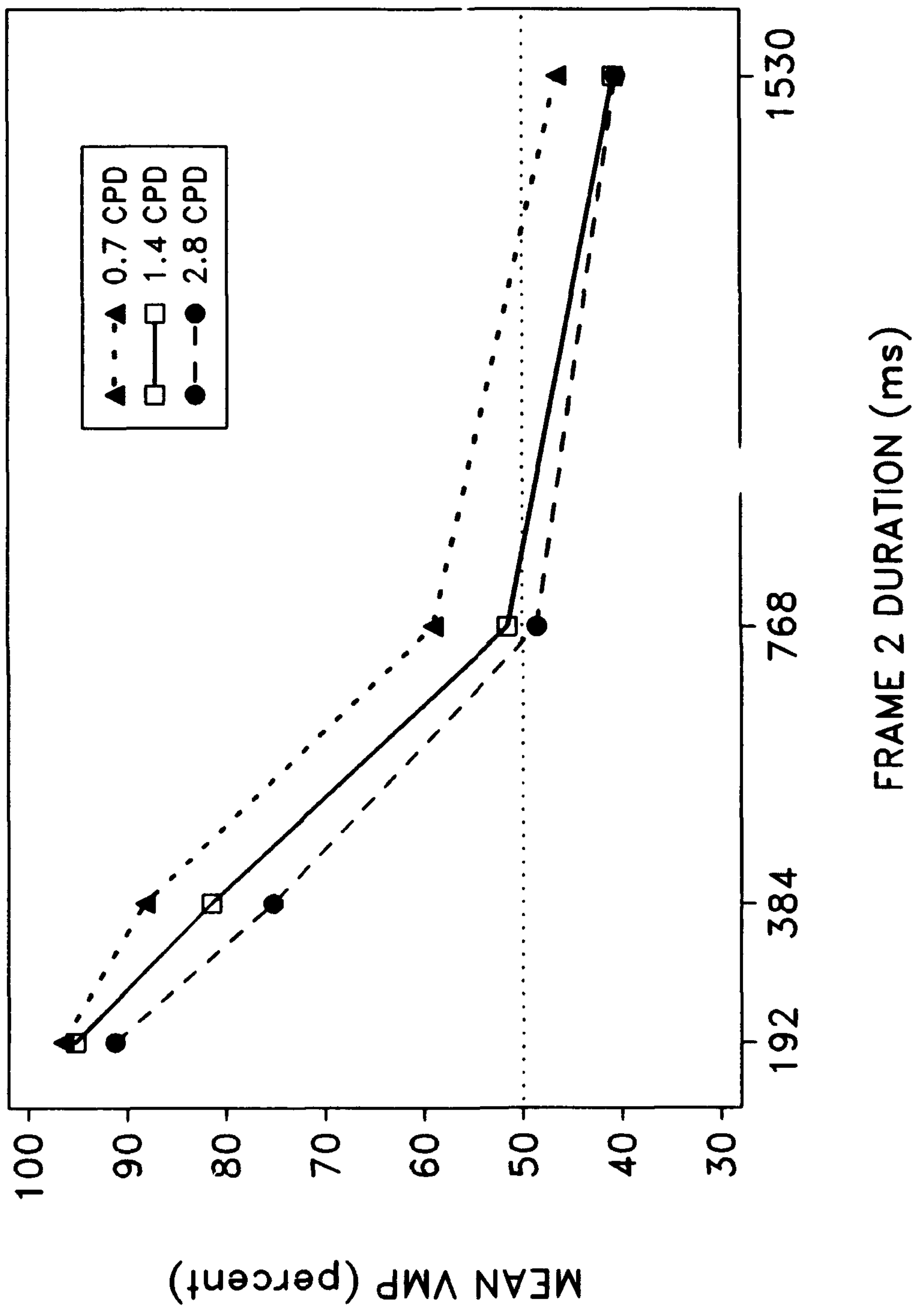

0.7 CPD
1.4 CPD
2.8 CPD
MEAN VMP (percent)
100
90
80
70
60
50
40
30
192
384
768
1530
FRAME 2 DURATION (ms)

Figure 12. Mean percent visual motion priming (VMP) as a function of frame 1 biaser contrast for low and high probe contrast conditions.

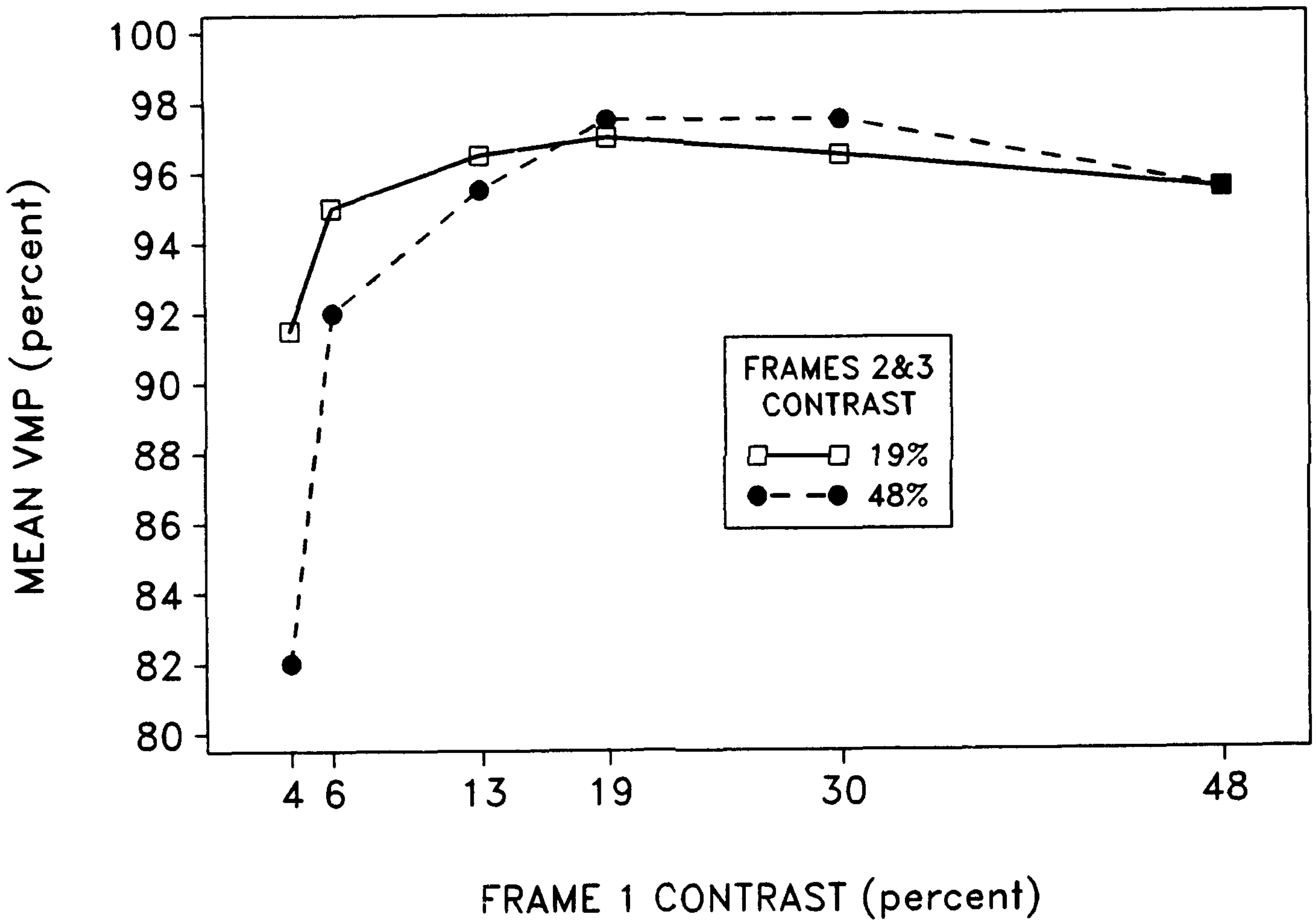
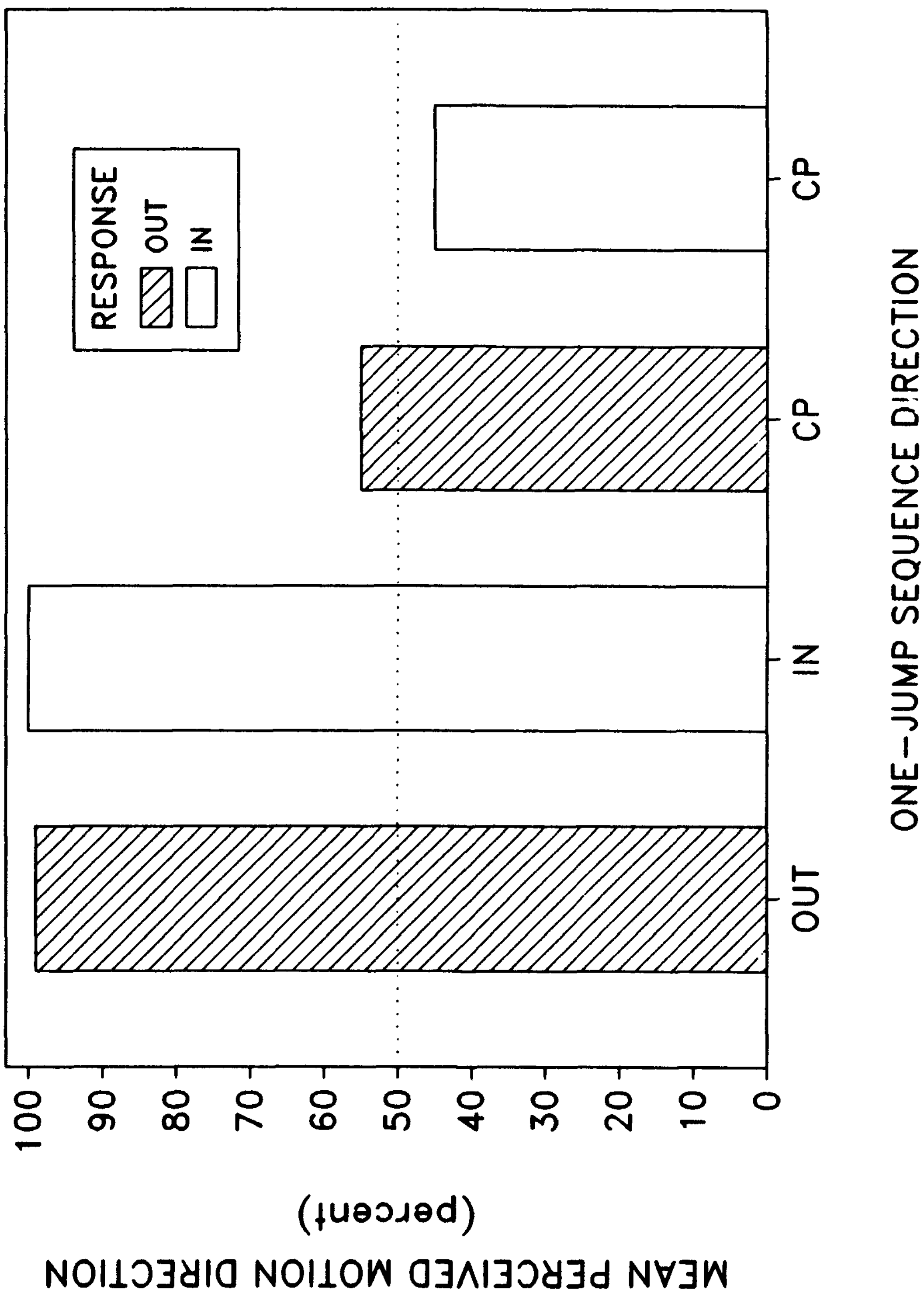

MEAN VMP (percent)
100
98
96
94
92
90
88
86
84
82
80
4
6
13
19
30
48
FRAME 1 CONTRAST (percent)
FRAMES 2&3
CONTRAST
19%
48%

Figure 13. Mean percent observed motion direction of one-jump, outward, inward, and counterphase (CP) split-field presentations.



MEAN PERCEIVED MOTION DIRECTION (percent)
0
10
20
30
40
50
60
70
80
90
100
ONE-JUMP SEQUENCE DIRECTION
OUT
IN
CP
CP
RESPONSE
OUT
IN

Figure 14. Mean percent observed motion direction of a two-jump, outward visual motion priming (VMP) split-field presentations.

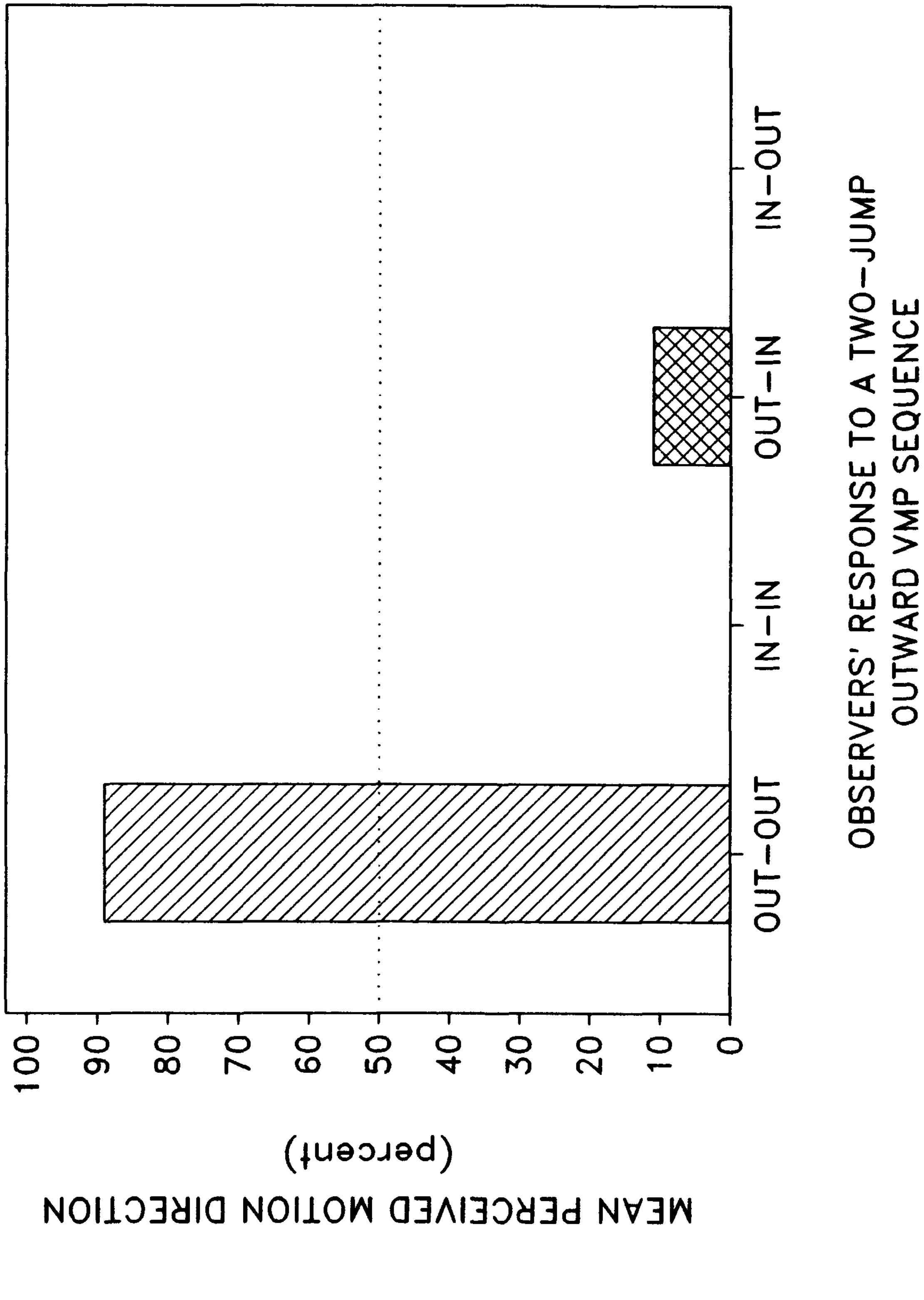

MEAN PERCEIVED MOTION DIRECTION
(percent)
0
10
20
30
40
50
60
70
80
90
100
OUT—OUT
IN—IN
OUT—IN
IN—OUT
OBSERVERS' RESPONSE TO A TWO—JUMP
OUTWARD VMP SEQUENCE

Figure 15. Mean percent observed motion direction of a two-jump, inward visual motion priming (VMP) split-field presentation.

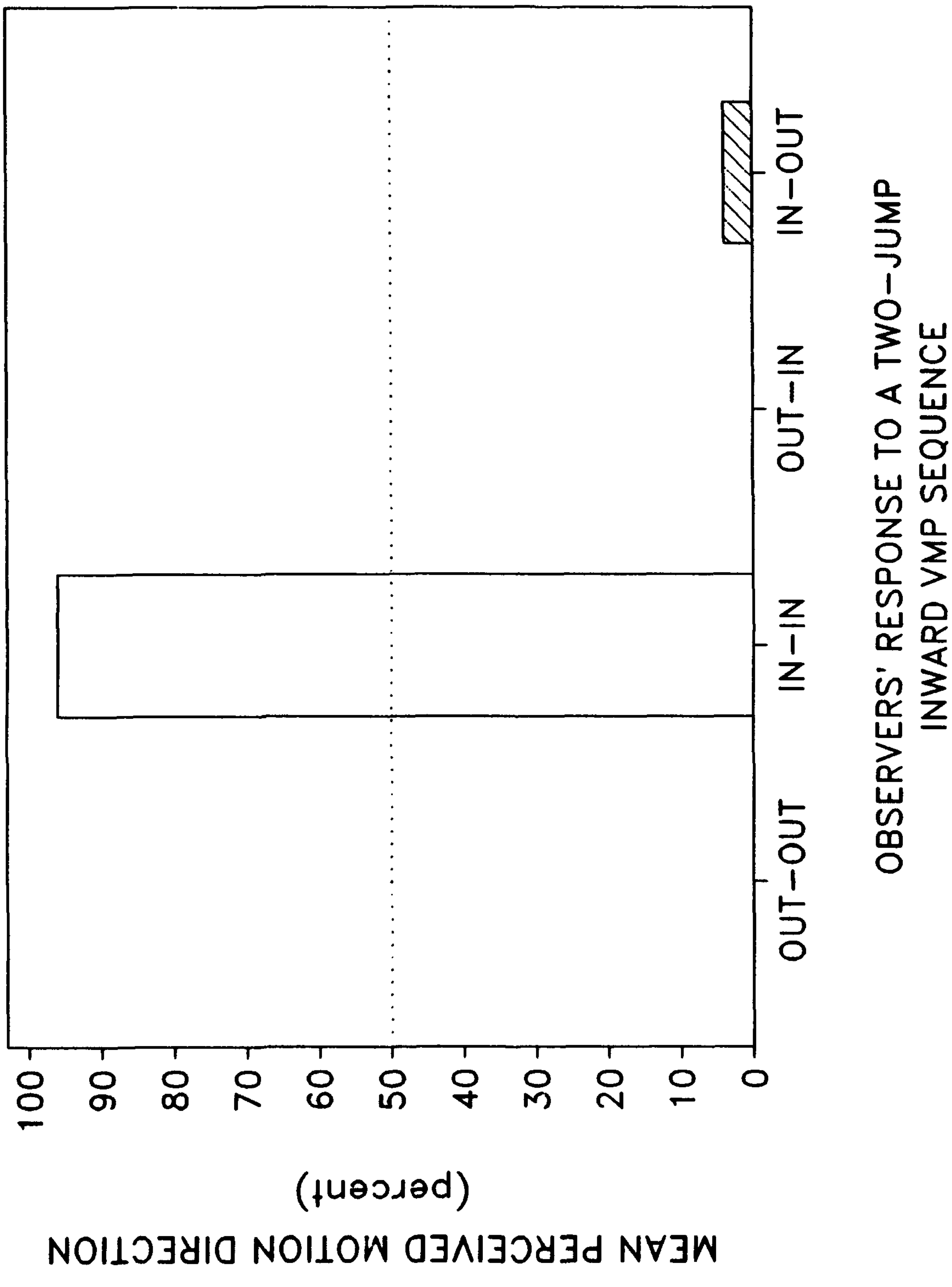

MEAN PERCEIVED MOTION DIRECTION
(percent)
0
10
20
30
40
50
60
70
80
90
100
OUT—OUT
IN—IN
OUT—IN
IN—OUT
OBSERVERS' RESPONSE TO A TWO—JUMP
INWARD VMP SEQUENCE

Figure 16. Mean percent observed direction of two-jump, counterphase, split-field presentations.

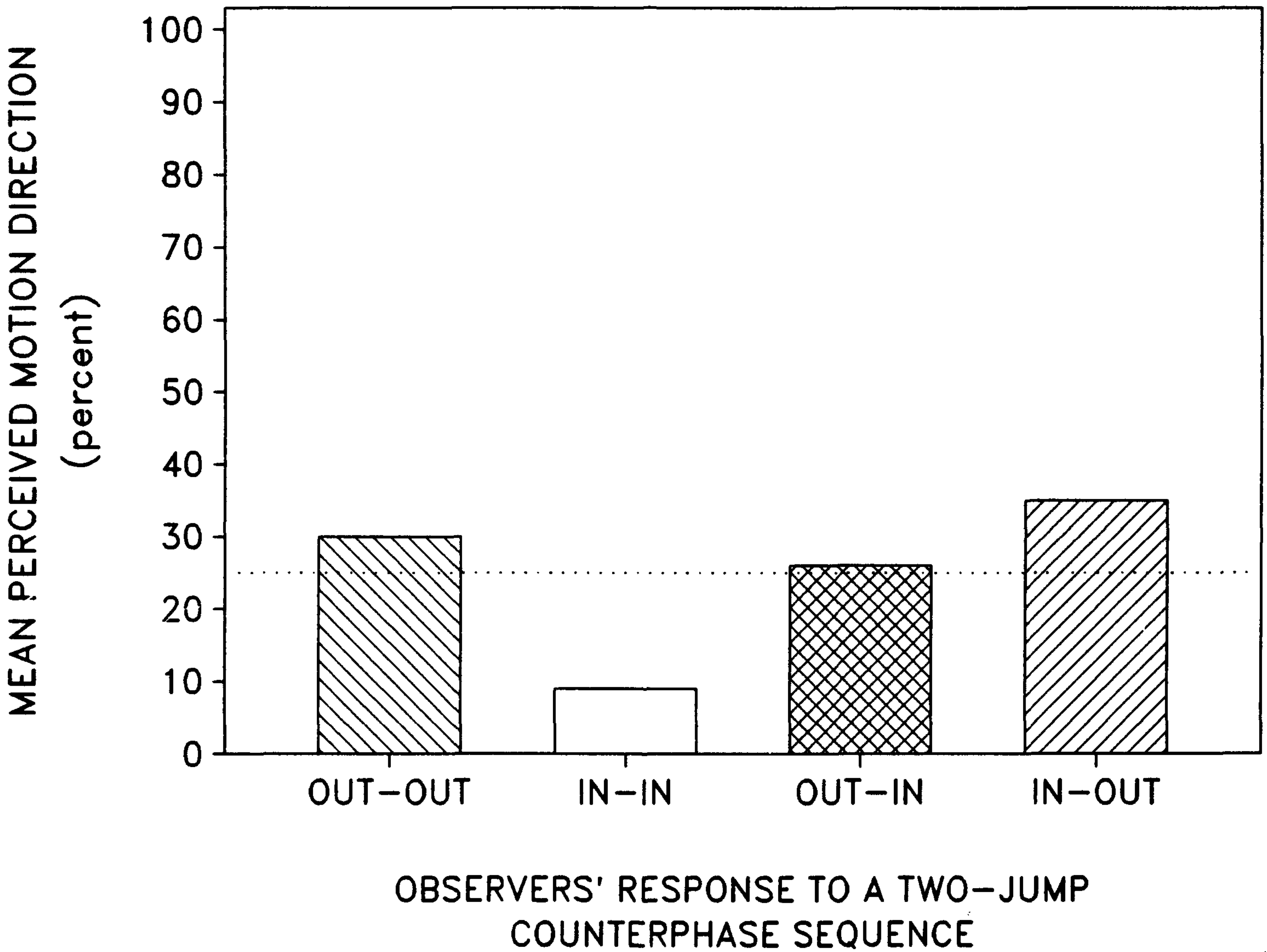

MEAN PERCEIVED MOTION DIRECTION
(percent)
100
90
80
70
60
50
40
30
20
10
0
OUT-OUT
IN-IN
OUT-IN
IN-OUT
OBSERVERS' RESPONSE TO A TWO-JUMP
COUNTERPHASE SEQUENCE

Figure 17. Impulse response of a Gaussian temporal integration filter.

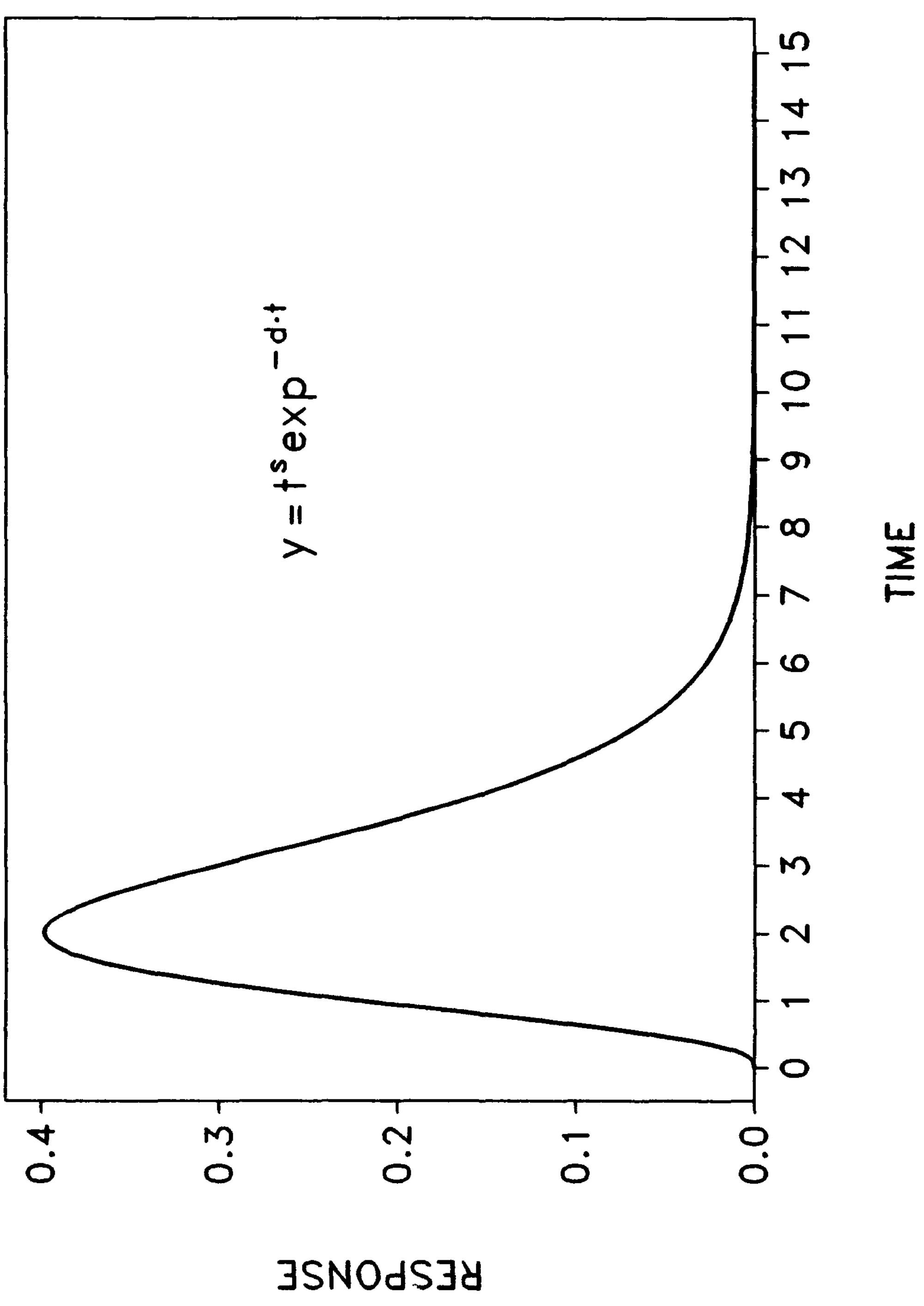

y = t^s exp^-d·t
TIME
RESPONSE
0.0
0.1
0.2
0.3
0.4
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

Figure 18. (a) Leftward and rightward subunit and opponent-energy outputs of an elaborated Reichardt detector utilizing a Gaussian temporal integration filter placed after the multiplicative stage, for a long frame 2 duration (> 500 ms), plotted as a function of time and in response to a visual motion priming sequence.

(b) Leftward and rightward subunit an opponent-energy outputs of an elaborated Reichardt detector utilizing a Gaussian temporal integration filter placed after the multiplicative stage, for a short frame 2 duration (< 500 ms), plotted as a function of time and in response to a visual motion priming sequence.

(c) Leftward and rightward subunit and opponent-energy outputs of an elaborated Reichardt detector utilizing a Gaussian temporal integration filter placed after the subtraction stage, for a short frame 2 duration (< 500 ms), plotted as a function of time and in response to a visual motion priming sequence.

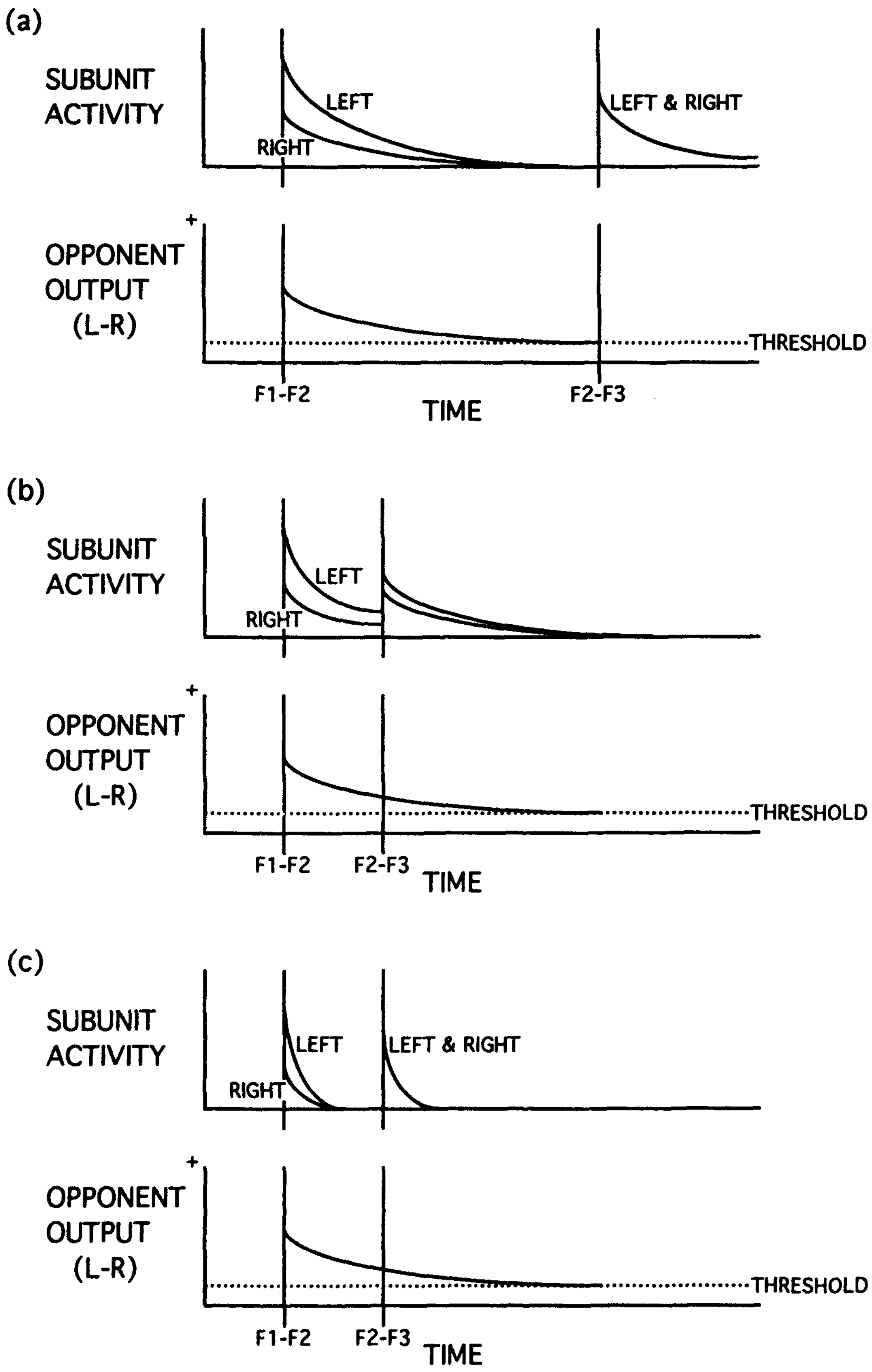
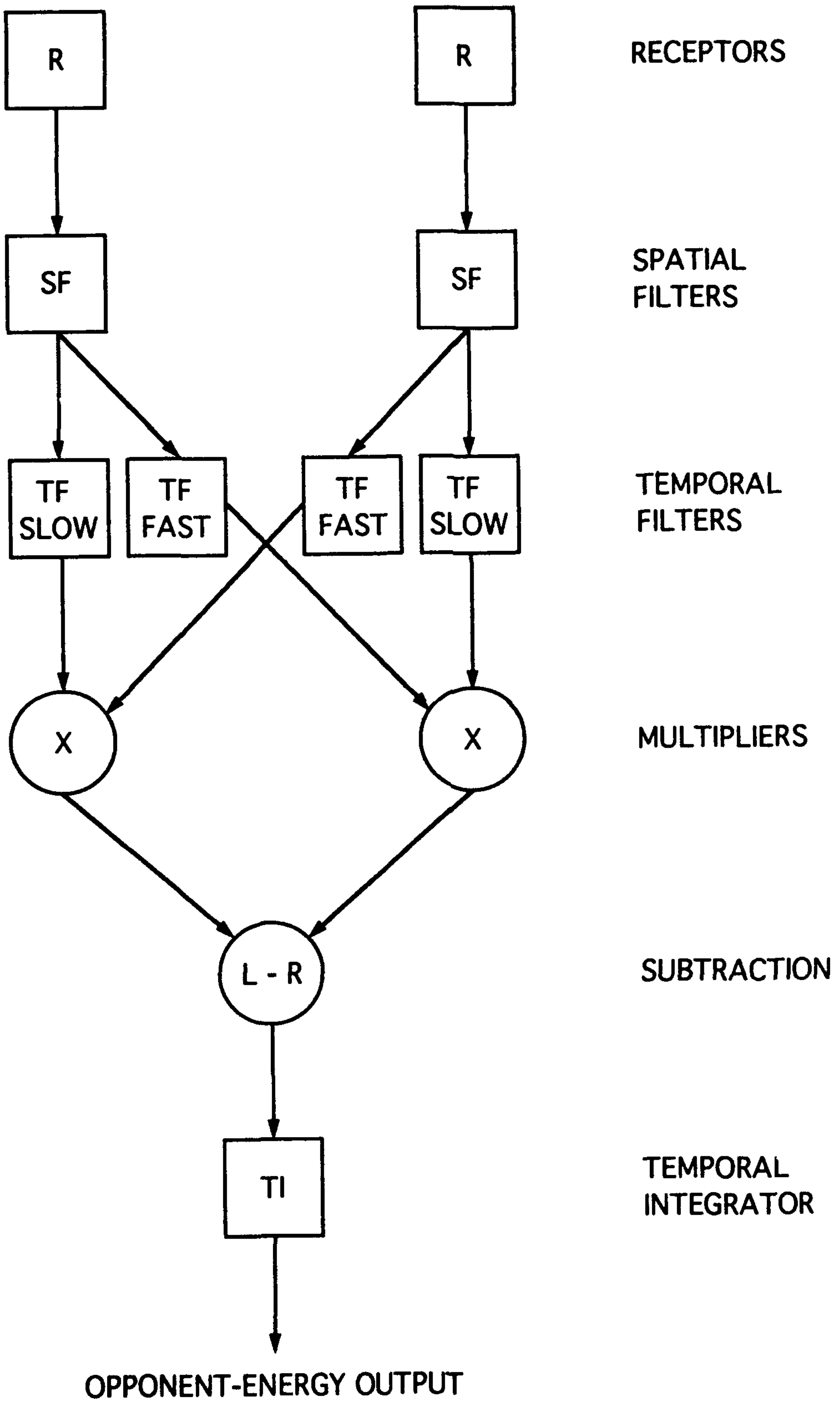

(a)
SUBUNIT ACTIVITY
LEFT
RIGHT
LEFT & RIGHT
OPPONENT OUTPUT (L-R)
+
THRESHOLD
F1-F2
F2-F3
TIME
(b)
SUBUNIT ACTIVITY
LEFT
RIGHT
OPPONENT OUTPUT (L-R)
+
THRESHOLD
F1-F2
F2-F3
TIME
(c)
SUBUNIT ACTIVITY
LEFT
LEFT & RIGHT
RIGHT
OPPONENT OUTPUT (L-R)
+
THRESHOLD
F1-F2
F2-F3
TIME

Figure 19. Elaborated Reichardt detector model with the temporal integration filter stage placed after the subtraction stage.


R
R
RECEPTORS
SF
SF
SPATIAL
FILTERS
TF
SLOW
TF
FAST
TF
FAST
TF
SLOW
TEMPORAL
FILTERS
X
X
MULTIPLIERS
L - R
SUBTRACTION
TI
TEMPORAL
INTEGRATOR
OPPONENT-ENERGY OUTPUT

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## APPENDIX 1

*Instructions to observers for Experiments 1, 2, and 3:*

This is a study in which you'll be making direction-of-motion judgments. Get comfortable, then don't move around. Keep a steady gaze on the screen throughout the session in order to stay adapted to its light level. Look at the center of the screen passively and as though you are looking through a window. Look at the entire pattern instead of a single bar. Don't try to follow the motion of the patterns with your eyes. Lock onto the vertical bars of the first pattern. All patterns are randomly presented; no special order. Go with your dominant feelings. Don't form any hypotheses, that is, don't try to figure it out. Ignore the various pattern changes, just report what you see. If you blink during a presentation, causing you to miss a jump, tell me and I will show you the pattern again. The display changes from a blank field, to bar patterns and then back to a blank. The rightward or leftward motions occur only in the bar patterns, not when the bars first appear or when they go off. Test conditions will be more difficult to judge but I will show you a few examples before we start. Sessions last about 15 minutes. There will be rest periods after each session. The first set of practice patterns are only a single left or right jump. The rest of the practice and test patterns will all be double-jump sequences. The double jumps can be *right/right, right/left, left/right,* or *left/left* directions. After the patterns have jumped, report their directions verbally. Speak clearly. Please don't discuss this experiment with any other potential subjects.

*Instructions to observers for Experiment 4 were the same as above except for the following changes:*

Patterns are split down the middle so the vertically oriented bars move either outward or inward. Fix your gaze centrally; use of position cues from the midline is not a reliable way for you to make your decisions. Practice trials are single jumps. The test will be a mixture of both 1- and 2-jump sequences. I will announce 1 jump or 2 jumps before each presentation. After the patterns disappear, report *out, in, out/out, out/in, in/out,* or *in/in.*